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ECOLOGICAL FACTORS AFFECTING THE ACTIVITY OF THE WESTERN FOX SQUIRREL, *SCIURUS NIGER RUFIVENTER* (GEOFFROY)

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ECOLOGICAL FACTORS AFFECTING THE ACTIVITY OF THE WESTERN FOX SQUIRREL, *SCIURUS NIGER RUFIVENTER* (GEOFFROY)

INTRODUCTION

The western fox squirrel, *Sciurus niger rufiventer* (Geoffroy), is one of the most important game animals in Iowa. It does not require extensive areas of unmolested timber, although it is a tree squirrel. Ecotones constitute the best habitats. These are represented by several types of plant associations. Upland stands of oak *(Quercus alba, Q. borealismaxima,* and *Q. macrocarpa)* and hickory *(Hicoria ovata)* near floodplain stands of black walnut *(Juglans nigra),* soft maple *(Acer saccharinum)* and elm *(Ulmus americana* and *U. fulva)* are desirable as sources of food and facilities for den nesting. Stands of mast-bearing trees bordering corn fields furnish the elements of protection. In addition they assure a more plentiful food supply during the mid-winter and late winter months when food supplies for many wild animals are at the lowest ebb.

In recent years extensive information has been presented about the biological factors influencing fox squirrel activity. Comparatively less is known of the meteorological and physiographical factors which affect the actions of the animal. The purpose of this investigation was to measure certain attributes of weather and time, and to determine the extent of their effects on the fox squirrel by using the degree of its activity as a gauge of effects.

The writer expresses his grateful appreciation to Dr. Halbert M. Harris, Head, Department of Zoology and Entomology, Iowa State College; Dr. Carl J. Drake, former Head, Department of Zoology and Entomology, Iowa State College; Dr. George O. Hendrickson, Associate Professor, Department of Zoology and Entomology, Iowa State College; and to Dr. Thomas G. Scott, former Leader of the Iowa Cooperative Wildlife Research Unit, U. S. Fish and Wildlife Service, for helpful suggestions and guidance in planning and accomplishing the research. H. C. S. Thom, Research Professor, Agronomy Department, Iowa State College, and Marvin Magnuson, Meteorologist, U. S. Weather Bureau, Des Moines, Iowa, contributed to interpretation of research by furnishing pertinent meteorological data.

INVESTIGATION

LOCALITY

The area chosen for the investigation consisted of approximately 250 acres located along Squaw Creek, its tributary, Onion Creek, and the vicinity nearby in Sections 29, 32 and 33 of Franklin Township, Story County, Iowa. About one-half the area under observation was posted against hunting. There was no change in this status throughout the course of the investigation. Observations were made from April, 1938 to March, 1941 and from February, 1946 to July, 1947.

Most of the area was subjected to grazing by cattle, sheep, or horses at one time or another. The heaviest grazing occurred on approximately 100 acres of floodplain. Lighter grazing occurred on about 40 acres of ridge-ravine topography; very light and intermittent grazing was permitted on about 90 acres of ridge-ravine area; and approximately 20 acres of the ridge-ravine type were grazed at no time.

The study area consisted of two major topographic types; floodplain and upland. The former supported an upper floodplain association with American elm, box elder *(Acer negundo),* black walnut, and red elm as the dominant tree species. The upland tracts supported two more or less segregated plant associations: oak-hickory and linden-maple. The oak-hickory association was composed of white oak, red oak, bur oak, shag-bark hickory, and bitternut *(H. cordiformis).* The linden-maple association supported black maple, linden, ironwood *(Ostrya virginiana),* red oak, American elm, butternut *(J. cinerea),* and serviceberry *(Amelanchier* sp.).

METHOD OF PROCEDURE

This research tests the hypothesis that the amount and type of squirrel activity are indicators of the interactions of meteorological, seasonal and topographical influences. The element of fluctuating population possibly exerts some influence as far as monthly and seasonal analyses of data are concerned; however, it is believed that the effect of this element is at a minimum for the following reasons: (1) Throughout the periods of observation only four hunting parties were encountered. (2) One squirrel constituted the known total take by man. (3) Approximately half the area was posted. (4) At no time was there a failure of the mast crop. (5) Any tendency of the population to migrate to other areas with a more plentiful food supply was minimized by the presence each year of corn fields adjoining the habitat. Supplements to mast and other foods were plentiful. (6) There was no evidence indicating other than normal population decimation from predators, disease, parasites, and accidents.

A measurement of activity was obtained by counting the number of squirrels seen. Two counting methods were used. The linear count consisted of recording the number of animals seen as the worker walked a course of estimated length and area. The spot count or time-area count consisted of recording the number of squirrels seen as the worker remained

at a certain spot for a definite length of time. Selected observation spots included all the types of topography represented under as wide a range of climatic and seasonal conditions as possible.

Regardless of the method used, the following data were recorded during each count attempt: date, time of day in the field, degree of overcast, number of squirrels seen, time at which squirrels were seen, locality (ridge, ravine, floodplain) on which squirrels were seen, distance walked during observations, acreage observed, % of defoliation, count method used, and supplementary remarks such as presence and depth of snow, presence of precipitation (rain, snow, hail, mist, fog), foraging and feeding activity especially in cultivated tracts, mating actions, nest-building activity, play and animality traits.

Meteorological data were obtained from various sources. The U. S. Weather Bureau Station at Des Moines, Iowa, furnished data on barometric pressure. The meteorological station at the Agronomy Farm, Iowa State College, contributed data on temperature, relative humidity, and precipitation. The writer obtained wind velocity data by taking readings with a windmill-type hand anemometer on the area and during the time observations were made.

Of all meteorological factors considered, wind velocity appeared to exhibit the most fluctuation within the smallest area. Consequently, on the spot data were essential. Averages of micro-climatic readings were used to obtain a single value of wind velocity for an observational period-area. Temperature, relative humidity, and precipitation displayed much less variation over relatively small areas; consequently, the writer did not attempt to secure micro-climatic readings for those three categories of data. Barometric pressure displayed the least variation over local areas with negligible change in altitude; hence, readings taken at the Des Moines weather station were deemed to be sufficiently accurate for this study.

FINDINGS

SEASON OF YEAR

Seasonal divisions were made arbitrarily in accordance with calendar divisions. Winter begins December 21 and ends March 20; spring, March 21 and June 20; summer, June 21 and September 20; and autumn, September 21 and December 20.

Reference to Table 1 shows that the numbers of 30-minute observation periods vary little from season to season. Quite evident from data obtained by spot count are the constant values of squirrels seen per hour during winter, spring, and summer. Autumn shows a decided increase. The number of squirrels seen per acre of observational area was least in winter and increased through spring to a summer and autumn maximum.

Data obtained from linear count indicate greater squirrel activity for all seasons than do data from spot count. This is especially true of winter and autumn. The ratios of squirrels seen per hour by linear count indicate a relatively large amount of

TABLE 1. Seasonal Relationship Among Observation Periods, Squirrels Seen and Acres.

Season	Number of 30-minute Periods	Number of Squirrels	Acres Observed	Squirrels an Hour	Squirrels an Acre
a. Spot count					
Winter	103	50	665	0.97	0.08
Spring	113	53	403	0.94	0.13
Summer	108	52	150	0.96	0.35
Autumn	113	140	374	2.48	0.37
b. Linear count					
Winter	97	135	2735	2.78	0.05
Spring	104	86	1760	1.65	0.05
Summer	102	76	700	1.49	0.11
Autumn	107	234	2460	4.37	0.10
c. Combined spot and linear counts					
Winter	200	185	3400	1.85	0.05
Spring	217	139	2163	1.28	0.06
Summer	210	128	850	1.22	0.15
Autumn	220	374	2834	3.40	0.13

TABLE 2. Monthly Relationship Among Observation Periods, Squirrels Seen and Acres.

Month	Number of 30-minute Periods	Number of Squirrels	Acres Observed	Squirrels an Hour	Squirrels an Acre
a. Spot count					
December	36	54	175	3.00	0.31
January	35	17	295	0.97	0.06
February	36	17	205	0.95	0.08
March	36	15	180	0.83	0.08
April	39	26	234	1.33	0.11
May	36	9	54	0.50	0.17
June	38	18	60	0.95	0.30
July	32	15	45	0.94	0.33
August	38	13	50	0.68	0.26
September	36	24	50	1.33	0.48
October	38	40	64	2.10	0.63
November	37	47	180	2.54	0.26
b. Linear count					
December	34	92	970	5.41	0.09
January	35	73	1035	4.17	0.07
February	34	27	1010	1.59	0.03
March	34	34	1240	2.00	0.03
April	31	33	660	2.13	0.05
May	35	28	210	1.60	0.13
June	34	20	200	1.18	0.10
July	38	18	315	0.95	0.06
August	30	26	210	1.73	0.12
September	34	37	205	2.18	0.08
October	38	70	665	3.68	0.11
November	33	73	935	4.43	0.08
c. Combined spot and linear counts					
December	70	146	1145	4.17	0.13
January	70	90	1330	2.57	0.07
February	70	44	1215	1.26	0.04
March	70	49	1420	1.40	0.03
April	70	59	894	1.69	0.07
May	71	37	264	1.04	0.14
June	72	38	260	1.06	0.15
July	70	33	360	0.94	0.09
August	68	39	260	1.15	0.15
September	70	61	255	1.74	0.34
October	76	110	729	2.89	0.15
November	70	120	1115	3.43	0.11

winter activity, lesser spring and summer activity of similar intensity, and peak activity in autumn. The ratios of squirrels seen to acres of observational area show a winter and spring minimum, a summer maximum, and a slightly lesser value for autumn.

Data obtained from spot and linear counts are combined into total count data to furnish a general interpretation of seasonal activity. The combined data show that fox squirrels are at a peak of activity in autumn. Winter shows a substantial decline; whereas, spring and summer show minimum and approximately equal activity.

MONTH OF YEAR

Evaluations of the amount of squirrel activity for each month are presented in Table 2. These values are expressed as ratios of the number of squirrels seen during any one month to the number of hours of monthly observation for that specific month. The degree of activity indicates a similar monthly trend for both spot and linear counts. Peak of activity is in December after a gradual increase from September through October and November. Minimum activity occurs during May, June, July, and August. Activity during February, March, and April is but slightly greater than it is during the summer months. Data for January furnish the only wide variation in amount of activity between the two count methods used. A discussion of the factors contributing to this variation is given in a subsequent section.

HOUR OF DAY

The effect which time of day exerts upon squirrel activity is given in Table 3 for spot, linear, and combined counts. Use of the spot method indicates the fox squirrel is most active from 6:00 A.M. to 1:00 P.M. with two activity peaks occurring from 7:00 A.M. to 8:00 A.M. and from 11:00 A.M. to 12:00 M. A late afternoon resurgence of activity occurs from 6:00 to 7:00.

These findings are rather closely complemented by data obtained from linear count. The latter indicates that most activity occurs between 6:00 A.M. and 2:00 P.M. with an almost continuous peak from 6:00 A.M. to 10:00 A.M. The linear count also shows an increase in activity from 6:00 P.M. to 7:00 P.M. There is relatively little activity between 2:00 P.M. and 6:00 P.M. Likewise, there is very little before sunrise and after sunset.

The combined data indicate that the fox squirrel has three major periods of activity during a day. The first period during which activity is most intense is from 7:00 A.M. to 8:00 A.M. The second period of slightly less intensity is from 11:00 A.M. to 12:00 M. The third period, much less than either of two foregoing periods, occurs from 6:00 P.M. to 7:00 P.M.

A further breakdown of data pertaining to time of day activity is made with respect to season in Table 4. This shows more information relative to daily activity with respect to each of the four seasons. Activity during winter appears to be greatest in forenoon, especially from 6:00 to 7:00 and from 8:00 to 9:00. However, this interpretation is derived from insufficient data. Slightly less activity is indicated between 12:00 M. and 2:00 P.M. Least activity occurs from 2:00 P.M. to 7:00 P.M. In spring, squirrel activity appears to attain peak intensity from 7:00 P.M. to 8:00 P.M. Relatively uniform activity intensity occurs from 5:00 A.M. to 11:00 A.M. Afternoon activity is concentrated between 4:00 and 8:00. Least activity occurs from 4:00 A.M. to 5:00 A.M. and from 2:00 P.M. to 4:00 P.M. Summer activity is greatest from 6:00 A.M. to 7:00 A.M. Secondary peaks occur from 8:00 A.M. to 9:00 A.M., 11:00 A.M. to 12:00 M., 1:00 P.M. to 2:00 P.M., and 6:00 P.M. to 7:00 P.M. Least activity is from 4:00 A.M. to 6:00 A.M., 2:00 P.M. to 6:00 P.M., and 7:00 P.M. to 8:00 P.M. Early morning activity in autumn is concentrated between 6:00 and 9:00. The most in-

TABLE 3. Time of Day Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Time of day	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
4 AM- 5 AM....	8	0	0.00	8	0	0.00	16	0	0.00
5 AM- 6 AM....	9	2	0.44	23	8	0.70	32	10	0.63
6 AM- 7 AM....	12	16	2.67	22	48	4.36	34	64	3.76
7 AM- 8 AM....	15	30	4.00	28	64	4.57	43	94	4.37
8 AM- 9 AM....	34	35	2.06	25	57	4.56	59	92	3.12
9 AM-10 AM....	72	64	1.78	26	62	4.76	98	126	2.57
10 AM-11 AM....	44	36	1.64	26	50	3.85	70	86	2.46
11 AM-12 M.....	18	35	3.89	27	50	3.71	45	85	3.78
12 M - 1 PM....	23	23	2.00	30	59	3.93	53	82	3.09
1 PM- 2 PM....	29	14	0.97	29	47	3.24	58	61	2.10
2 PM- 3 PM....	70	10	0.29	34	14	0.82	104	24	0.46
3 PM- 4 PM....	47	8	0.34	25	12	0.96	72	20	0.56
4 PM- 5 PM....	14	3	0.43	27	10	0.74	41	13	0.63
5 PM- 6 PM....	18	4	0.44	33	16	0.97	51	20	0.78
6 PM- 7 PM....	15	13	1.73	30	28	1.87	45	41	1.82
7 PM- 8 PM....	9	2	0.44	17	6	0.71	26	8	0.62

TABLE 4. Time of Day Relationship Between Number of Observation Periods and Number of Squirrels Seen by Combined Count.

Time of day	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Time of day	Number of 30-minute periods	Number of squirrels	Squirrels an hour
AM	**(a) WINTER**			**AM**	**(c) SUMMER**		
6- 7....	1	2	4.00	4- 5....	8	0	0.00
7- 8....	2	1	1.00	5- 6....	10	2	0.40
8- 9....	6	13	4.34	6- 7....	7	11	3.14
9-10....	20	24	2.40	7- 8....	..	..	....
10-11....	18	20	2.22	8- 9....	11	10	1.82
11-12....	19	17	1.79	9-10....	13	8	1.23
				10-11....	4	3	1.50
				11-12....	5	5	2.00
PM				**PM**			
12- 1....	37	64	3.46	12- 1....	6	4	1.33
1- 2....	16	29	3.63	1- 2....	17	17	2.00
2- 3....	37	8	0.43	2- 3....	21	11	1.05
3- 4....	19	3	0.32	3- 4....	25	11	0.88
4- 5....	9	0	0.00	4- 5....	17	6	0.71
5- 6....	15	4	0.53	5- 6....	19	10	1.05
6- 7....	1	0	0.00	6- 7....	25	27	2.16
				7- 8....	22	3	0.27
AM	**(b) SPRING**			**AM**	**(d) AUTUMN**		
4- 5....	8	0	0.00	5- 6....	10	0	0.00
5- 6....	10	8	1.60	6- 7....	15	37	4.94
6- 7....	11	10	1.82	7- 8....	30	83	5.54
7- 8....	11	10	1.82	8- 9....	19	47	4.95
8- 9....	23	22	1.91	9-10....	36	67	3.72
9-10....	29	27	1.86	10-11....	29	44	3.03
10-11....	19	19	2.00	11-12....	15	61	8.14
11-12....	6	2	0.66				
PM				**PM**			
12- 1....	..	..	....	12- 1....	10	14	2.80
1- 2....	15	11	1.47	1- 2....	10	4	0.80
2- 3....	35	3	0.17	2- 3....	14	3	0.43
3- 4....	23	3	0.26	3- 4....	4	2	1.00
4- 5....	4	3	1.50	4- 5....	9	4	0.89
5- 6....	7	5	1.43	5- 6....	10	1	0.20
6- 7....	12	11	1.83	6- 7....	7	7	2.00
7- 8....	2	5	5.00	7- 8....	2	0	0.00

tense activity occurs from 11:00 A.M. to 12:00 M. A secondary peak of activity is evident from 6:00 P.M. to 7:00 P.M. The periods from 1:00 P.M. to 6:00 P.M. and 7:00 P.M. to 8:00 P.M. show least activity. The data for each season except spring indicate that squirrel activity is greatest in the forenoon and is least in mid-afternoon.

TEMPERATURE

Although observations of squirrel activity were made at temperatures ranging from 0°F to 99°F, the relationships between the above two temperatures and number of squirrels seen per hour should be discounted, because the number of observation periods at temperatures below 15°F and above 89°F is insufficient to yield reliable information (Table 5). Both spot and linear counts indicate that the optimum temperature for squirrel activity lies within the limits of 40°F to 49°F. Secondary peaks of activity occur within ranges of 20°F to 24°F for both count methods and from 85°F to 94°F for linear count. Both methods of observation show decreased activity from 50°F to 84°F.

Undoubtedly the effects of other weather factors as well as seasonal factors are included but are more or less concealed in the data presented in Table 5. These data include the effects of two major aspects, daily and seasonal. In an attempt to evaluate more accurately the possible effects of temperature by itself, a seasonal classification of temperature is made in which the relationship between the number of squirrels seen per hour and the mean hourly temperature is shown for each of the four seasons. Mean hourly temperature was derived by recording the temperature of each observation period falling within a specific hour for a whole season, adding the temperatures, and dividing the sum by the number of observation periods. The relation of squirrels seen per hour to mean hourly temperature is given in Figures 1, 2, 3, and 4. In general, the graphs show that daily temperature at any season increases from an early morning or forenoon low to a maximum usually in fore- or mid-afternoon. On the other hand, it was mentioned previously that daily squirrel activity is at a maximum early in the forenoon and is least during early or mid-afternoon. These data suggest that intensity of activity may be directly proportional to a generalized temperature range as modified by season, and inversely proportional to other temperatures at different times of the day even though the latter temperatures equal or are higher or lower than those in direct proportion to activity.

For example, in winter the greatest squirrel activity occurs at temperatures between 15°F and 30°F, although there are four mean hourly temperatures between 31°F and 40°F, two of which are accompanied by relatively intense activity, the third by very little activity, and the fourth by no activity. In spring, activity is most intense at temperatures between 40°F and 70°F and is relatively less at temperatures exceeding 70°F. Summer shows three mean hourly temperatures in consecutive diurnal progression, each of which is between 65°F and 70°F. One of these means is accompanied by greatest summer activity, the second shows very little activity, and the third is accompanied by no activity. In autumn, greatest activity occurs within the temperature range of 35°F to 45°F. Also, during three hours of the day when activity is at its lowest ebb, the corresponding mean hourly temperatures are bracketed between 45°F and 55°F. Undoubtedly temperature influences squirrels, but in attempting to ascribe its effects one must include both the daily and seasonal aspects as well as the other meteorological factors with which temperature interacts.

RELATIVE HUMIDITY

Data for humidity are presented in groups of 10 units each. The relation of squirrels seen per hour is given for spot, linear and combined counts in Table 6. From this table it is seen that variations in the amount of squirrel activity at humidities ranging from the 20 to 29% bracket to the 80 to 89% bracket are noticeably similar for both spot and linear counts. However, humidities from 90 to 100% appear to

TABLE 5. Temperature Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Degrees Fahrenheit	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
0- 4............	2	3	3.00	..	..	....	2	3	3.00
5- 9............	2	2	2.00	4	7	3.50	6	9	3.00
10-14............	6	1	0.33	..	..	....	6	1	0.33
15-19............	17	6	0.71	14	13	1.86	31	19	1.23
20-24............	34	26	1.53	14	28	40.0	48	54	2.25
25-29............	18	10	1.11	23	25	2.17	41	35	1.71
30-34............	32	24	1.50	28	40	2.86	60	64	2.13
35-39............	26	14	1.08	53	76	2.87	79	90	2.28
40-44............	43	52	2.42	29	78	5.38	72	130	3.61
45-49............	16	28	3.50	26	41	3.16	42	69	3.28
50-54............	17	17	2.00	44	70	3.18	61	87	2.85
55-59............	17	8	0.94	25	30	2.40	42	38	1.81
60-64............	27	12	0.89	17	17	2.00	44	29	1.32
65-69............	35	29	1.66	29	24	1.66	64	53	1.66
70-74............	39	22	1.13	27	23	1.70	66	45	1.36
75-79............	34	14	0.82	42	30	1.43	76	44	1.16
80-84............	42	20	0.95	17	9	1.06	59	29	0.98
85-89............	17	6	0.71	11	13	2.36	28	19	1.36
90-94............	5	1	0.40	6	7	2.33	11	8	1.45
95-99............	8	0	0.00	1	0	0.00	9	0	0.00

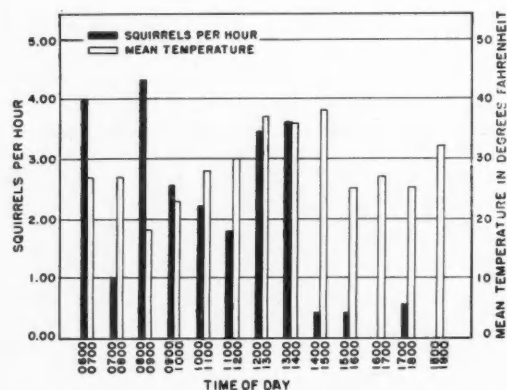FIG. 1. Relation of squirrels seen per hour to mean hourly temperature for winter.

FIG. 2. Relation of squirrels seen per hour to mean hourly temperature for spring.

exert a dissimilar effect upon degree of activity as adjudged by the two methods of observation.

Greatest squirrel activity, as observed by linear count, occurs at 100% relative humidity. However, such an interpretation probably should be discounted, because too few observations were made at that humidity condition to warrant an accurate use of the data. At the same humidity, observations by spot count point to much less activity. Likewise, one should be circumspect in interpreting spot count data at 100% humidity at their face value for lack of sufficient observation periods. Activity ratios for both spot and linear counts within the 20 to 29% bracket are also unreliable because they are supported by insufficient observation time.

Both count methods indicate that least animal ac-

tivity occurs at relative humidities between 20 and 39%. Each complements the other to show that an activity peak occurs at humidities from 50 to 59%. Degree of movement at humidities from 80 to 89% is similar for both count methods. However, this amount of movement is relatively high for all spot count data; whereas, compared with degree of activity for other linear count data, it is considerably less than maximum.

WIND VELOCITY

Most of the observations were made under air movement conditions that could be described generally

Fig. 3. Relation of squirrels seen per hour to mean hourly temperature for summer.
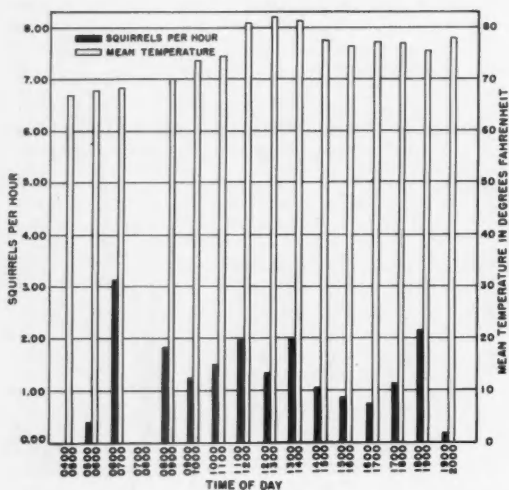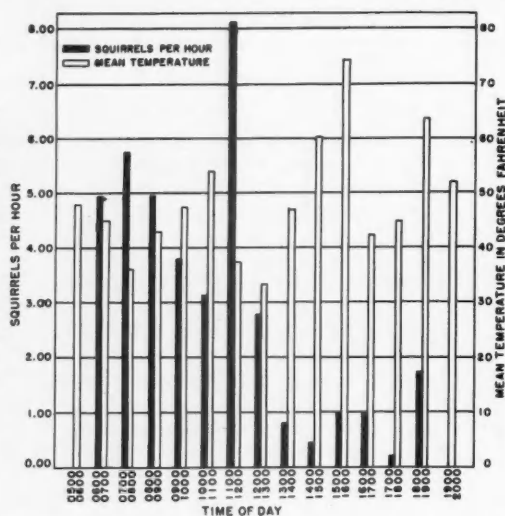

Fig. 4. Relation of squirrels seen per hour to mean hourly temperature for autumn.

TABLE 6. Relative Humidity Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Relative humidity	A. Spot Count			B. Linear Count			C. Combined Spot and Linear Counts		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
20-29	9	2	0.45	2	0	0.00	11	2	0.36
30-39	47	15	0.64	21	15	1.43	68	30	0.88
40-49	61	35	1.15	52	53	2.04	113	88	1.56
50-59	59	56	1.90	5	82	3.28	109	138	2.53
60-69	99	41	0.83	82	120	2.93	181	161	1.78
70-79	61	49	1.61	68	80	2.35	129	129	2.00
80-89	45	51	2.27	60	73	2.43	105	124	2.36
90-99	50	42	1.68	74	105	2.84	124	147	2.37
100	6	4	1.33	1	3	6.00	7	7	2.00

TABLE 7. Wind Velocity Relationships Between Number of Observation Periods and Number of Squirrels Seen.

Wind velocity in miles an hour	A. Spot Count			B. Linear Count			C. Combined Spot and Linear Counts		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
1	31	31	2.00	31	59	3.81	62	90	2.90
2	22	28	2.54	36	73	4.05	58	101	3.48
3	49	52	2.12	64	76	2.37	113	128	2.26
4	79	40	1.01	72	91	2.53	151	131	1.74
5	75	62	1.65	67	99	2.96	142	161	2.27
6	49	29	1.18	67	52	1.55	116	81	1.40
7	48	21	0.88	27	29	2.15	75	50	1.33
8	45	17	0.76	22	31	2.82	67	48	1.43
9	25	10	0.80	10	8	1.60	35	18	1.03
10	6	4	1.33	5	3	1.20	11	7	1.27
11	4	0	0.00	2	4	4.00	6	4	1.33
12	4	1	0.50	5	1	0.40	9	2	0.44
15	..	..	....	2	5	5.00	2	5	5.00

as quiet, breezy, or windy. Relatively few observations were made under conditions of high wind.

Data grouped by spot, linear, and combined counts are presented in Table 7. The majority of observations were made at wind velocities of from one to nine miles per hour. No observations by either spot or linear count were made in wind velocities exceeding 12 miles per hour with the exception of two 30-minute linear count periods in a wind velocity of 15 miles per hour.

Data in Table 7 show that the effect of wind velocity upon squirrel activity exhibits approximately proportional variation in spot and linear data from velocities of one mile per hour to and including six miles per hour. At higher velocities, especially at 11 and 15 miles per hour, the data acquired by the two methods are strikingly dissimilar.

Each count method indicates that greatest squirrel activity occurs in winds of from one to two and two to three miles per hour. Greater velocities cause a decrease in the amount of activity. Several phenomena are evident at wind velocities greater than 10 miles per hour. These are considered in more detail in the discussion section.

BAROMETRIC PRESSURE

Readings of barometric pressure for all data range from 29.44 inches to 30.62 inches except there are no pressure readings from 30.50 inches to 30.59 inches. The readings are aggregated into groups of ten-hundredths. They are presented in Table 8. Because the number of observation periods with pressure readings below 29.60 inches and above 30.49 inches is relatively small compared with groupings of the remaining readings, it is deemed inadvisable to infer significance from the relationships of pressure in these two brackets to squirrel activity.

Discounting the possible inferences of the two pressure groups for which sufficient data are lacking, it appears that degree of activity is, in general, related proportionally to magnitude of pressure. This is

true of observations made by both spot and linear count methods. However, data by linear count show a greater increase of activity with increase of pressure than do data derived by spot count. In both methods a relatively small amount of activity occurs at pressures from 29.60 inches to 29.69 inches, and relatively intense activity takes place at pressures from 30.40 inches to 30.49 inches.

DEGREE OF OVERCAST

The amount of overcast is arbitrarily divided into three categories: cloudy, partly cloudly and clear. Classification of the overcast conditions was made on the following basis. If the sun was obscured by clouds throughout the observation period, the condition was designated cloudy. If the sun was partially obscured during the observation period, the degree of overcast was designated partly cloudy. This condition ranged from almost complete cloudiness to almost complete clearness. A classification of clear was given if the sun was completely unobscured by clouds during the whole period of observation.

The relation of degree of overcast to squirrel activity is given for spot, linear and combined data in Table 9. In the spot count method the least activity occurs in cloudy weather. The amount of activity increases during partly cloudy weather and reaches a maximum when skies are clear.

The ratios of number of squirrels to number of hours of observation for linear count are respectively greater than the corresponding ratios for spot count. This is to be expected because a larger area is observed during one hour of linear count than during one hour of spot count.

The ratios obtained from linear count data indicate that squirrel activity is least during cloudy weather, increases under partly cloudy conditions, and is greatest during clear weather. A similar interpretation can be made from combined data; however, in the latter case the variation in amount of activity during

TABLE 8. Barometric Pressure Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Barometric pressure in inches	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
29.40-29.49	..	..	....	1	1	2.00	1	1	2.00
29.50-29.59	4	8	4.00	1	2	4.00	5	10	4.00
29.60-29.69	21	10	0.95	10	4	0.80	31	14	0.90
29.70-29.79	45	35	1.56	29	38	2.62	74	73	1.97
29.80-29.89	67	31	0.93	54	60	2.22	121	91	1.50
29.90-29.99	84	61	1.45	91	101	2.22	175	162	1.85
30.00-30.09	58	31	1.07	66	86	2.61	124	117	1.89
30.10-30.19	60	57	1.90	89	124	2.79	149	181	2.43
30.20-30.29	46	26	1.13	41	73	3.56	87	99	2.28
30.30-30.39	36	15	0.83	19	33	3.48	55	48	1.75
30.40-30.49	16	21	2.62	3	5	3.33	19	26	2.74
30.50-30.59	..	..	....	..	..	....	..	..	....
30.60-30.69	..	..	...	6	4	1.33	6	4	1.33

partly cloudy and clear conditions is not so pronounced as it is for linear count data.

PRECIPITATION

Data concerning precipitation are divided into rain and snow. Included in rain are thunder showers, drizzles and mists. A few instances of sleet are grouped with snow.

Data for spot, linear and combined counts are presented in Table 10. An examination of data shows that fox squirrel activity during rain is greater by spot count than by linear count. Activity during snow shows a converse relationship between the two count methods. Data for the two counts combined show that activity is slightly less in rain than in snow, and that activity is greater when there is no

precipitation than when rain or snow is falling. No observations were made during exceptionally heavy and prolonged rains. However, observations were made during heavy snowfall and blizzards.

DEPTH OF SNOW

A comparison is made in Table 11 of squirrel activity in various snow depths from data obtained by spot and linear count. In addition to data for various snow depths, figures are presented for the two categories, "no snow" and "patches of snow."

Examination of data shows little agreement between spot and linear count other than an indication that degree of squirrel activity is not noticeably affected by a snow depth up to and including two inches. Snow deeper than two inches reduced the amount of

TABLE 9. Degree of Overcast Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Degree of overcast	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
Cloudy.........	104	66	1.27	147	148	2.08	251	214	1.71
Partly cloudy....	66	44	1.33	68	89	2.62	134	133	1.98
Clear............	267	185	1.39	195	294	3.02	462	479	2.08

TABLE 10. Precipitation Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Precipitation	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
Raining.........	25	20	1.60	33	14	0.85	58	34	1.17
Snowing.........	12	1	0.17	24	27	2.25	36	28	1.56
Total precipitation	37	21	1.14	57	41	1.44	94	62	1.32
No precipitation..	400	274	1.37	353	490	2.78	753	764	2.03

TABLE 11. Depth of Snow Relationship Between Number of Observation Periods and Number of Squirrels Seen.

Depth of snow in inches	A. SPOT COUNT			B. LINEAR COUNT			C. COMBINED SPOT AND LINEAR COUNTS		
	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour	Number of 30-minute periods	Number of squirrels	Squirrels an hour
Patches..........	48	27	1.12	37	78	4.22	85	105	2.47
1..............	4	0	0.00	22	28	2.55	26	28	2.16
2..............	..	..	....	11	19	3.46	11	19	3.46
3..............	4	0	0.00	9	8	1.78	13	8	1.23
4..............	4	1	0.50	9	3	0.67	13	4	0.62
5..............	..	..	....	5	3	1.20	5	3	1.20
6..............	20	9	0.90	..	..	....	20	9	0.90
7..............	8	4	1.00	..	..	....	8	4	1.00
11.............	4	0	0.00	1	1	2.00	5	1	0.40
12.............	2	0	0.00	3	3	2.00	5	3	1.20
No snow.........	343	254	1.48	313	388	2.48	656	642	1.96

activity considerably. Both count methods indicate that squirrels are as active or more active when patches of snow are on the ground as when the ground is covered by any snow depth presented in Table 11.

DISCUSSION

Attempts to explain certain phenomena of squirrel activity are difficult because only in a very few instances does the writer believe a specific ecological factor is sufficiently isolated from the interactions of other factors to justify the statement that an activity phenomenon is attributable to the effect of only one factor. Indeed, the fox squirrel is most active in autumn. The reasons for this are to be found in a consideration of several ecological conditions.

The food supply is most plentiful during the autumn months. Coupled with this fact is the instinctive tendency of the fox squirrel to store food for winter use. Another factor to be considered is normal autumn temperature. This season is not so subject to temperature extremes as are summer and winter. Consequently, the fox squirrel is more active when it does not encounter extreme heat or cold.

In the section on method of procedure, it was stated that the attributes of a fluctuating population possibly exert some influence upon an analysis of seasonal data. This appears to be the case, especially concerning fall activity. Young of the year are fully active at this time and contribute to population increase, which must be considered in evaluating magnitude of activity.

Another condition which should be mentioned is the amount of defoliation. Late spring, all of summer and a very short time in early autumn have complete foliation. This reduces observational area for both spot and linear counts to about one-sixth that of winter. If areas observed were the same at all seasons, winter, spring and fall would probably yield data indicating relatively less activity.

The disagreement between spot and linear measurements of activity in winter is attributable for the most part to one abnormal condition of weather. There was unusually warm weather in January, 1947. In the Des Moines area over 100 degrees excess to normal mean accumulated that month. With the normal mean for most of January at 21°F, five observations were made at temperatures in the fifties, four in the forties and one in the thirties. Most of these observations were made by linear count. Undoubtedly, these unseasonably high temperatures were instrumental in causing greater animal activity and reflected a value for linear count substantially greater than that for spot count. On the other hand, Goodrum (1937) mentioned inclement weather and diminishing food supply as partial reasons for seclusion of both the Texas gray squirrel *(Sciurus carolinensis carolinensis)* and fox squirrel *(Sciurus niger limitis)* after the winter mating season. Baumgartner (1934) discussed seasonal movement of the fox squirrel *(Sciurus niger rufiventer)* with reference to the breeding season. Throughout December and early in January, and again in May, he noticed a general unrest

in a given squirrel population. According to the investigation of Baker (1944) in eastern Texas, ripening of the mast crop in late September and October was responsible for increased tree squirrel aggregation which developed to a peak visible population in December.

Seasonal tendencies discussed above are partially substantiated by monthly data given in Table 2. Also, the influence of the amount of defoliation upon animal per area values can be readily seen from this table. The variation ranges from complete foliation in June, July, August and September to about 95% defoliation in November, December, January, February and March. Defoliation is not complete during these months because the white oak retains most of its leaves throughout winter and into April. Gradations between complete foliation and almost complete defoliation occur during other months of the year. In addition to the amount of tree defoliation, the amount of shrub defoliation is also important in its capacity to conceal squirrel activity at understory and ground levels.

The investigation of magnitude of activity with respect to time of day is also complicated by the simultaneous influences of several factors. Observations were confined for the most part to hours between sunrise and sunset. A few field trips were made at pre-dawn when light was sufficient to reveal the contours of trees and buildings only when they were seen against the eastern horizon. At this time diurnal birds were active by calls and songs, but there was no evidence of squirrel activity either by sight or hearing. A few squirrels were observed and heard in the light of dawn just before sunrise. It was not until after sunrise, as the usual case, that the squirrels began their daily activity.

Animal activity cycles on a 24-hour basis have received considerable attention in recent years. Calhoun (1944, 1946) in his consolidation of literature pertaining to animal periodicities applied the terms diurnal, nocturnal, crepuscular, and arythmic to distinguish the major activity rhythms. Some of the conclusions he presented are especially interesting in their application to the activity cycles of rodents, especially the fox squirrel. Morphological and anatomical adaptations favoring diurnality rather than nocturnality or crepuscular activity are presented by Walls (1942). According to Welsh (1938) the cyclic manifestations of animal activity are caused in a normal environment by recurring external factors. Park (1940) stated that dawn and dusk are the two parts of the daily cycle when relatively great activity changes are initiated in the majority of animals. Hatt (1929) reported that red squirrels *(Sciurus hudsonicus gymnicus* and *S. h. loquax)* were usually active throughout daylight. From information gathered by Klugh (1927) it appeared that the red squirrel was active throughout the day from sunrise to twilight. Nocturnal activity was reported by Merriam (1884) and Nelson (1918). Hamilton (1939) in census studies of the red squirrel *(Tamiasciurus hudsonicus)* on the Cornell University campus

found the animals exhibited two daily peaks of activity. Greatest activity was observed between 6:00 A.M. and 8:00 A.M. and a secondary peak was noticed at about one hour before sunset. In a study of tree squirrels of eastern Texas, Baker (1944) made counts from daylight to two and one-half hours after sunrise. In Allen's (1942) observations on the fox squirrel in Michigan he found no evidence of other than daylight activity. Data presented by Brown & Yeager (1945) indicated that the daily activities of gray and fox squirrels in Illinois were most intense during early forenoon. According to Seton (1929) 10:00 A.M. or 11:00 A.M. is the fox squirrel's favorite time of day to be abroad.

The writer found that a slump in daily activity begins at about 2:00 P.M. and continues until about 6:00 P.M. Probably temperature is the major factor. It is not uncommon at any season of the year for the highest daily temperature to occur at this time or approximately so. In summer such a condition might well be responsible for lethargy and rest. Late afternoon or early evening, depending upon the season, appears to be a time for feeding and general resumption of activity. More movement appears to continue into evening than occurs at dawn with similar light intensity. In either case the element of inertia exerts some influence. Several observations were made at evening dusk but very little activity was noticed. No observations were made between 9:00 P.M. and 3:00 A.M. However, from observations made at dawn and evening dusk, it is fairly evident that the fox squirrel is diurnal. This observation corroborates that made by Allen (1942). The general activity pattern of the fox squirrel is resolved into relatively intense forenoon activity, much less afternoon activity and late afternoon or evening activity of secondary magnitude. Since the fox squirrel is diurnal, this pattern is anticipated from the animal periodicity studies made by Calhoun (1944).

Daily activity appears to be associated with season. In addition to the relatively intense forenoon activity for all seasons, there are separate, relatively isolated peaks of activity occurring at different hours of the day in each season. These somewhat isolated activity peaks which may or may not conform to the general activity pattern must be interpreted rather carefully when they are substantiated by only a relatively small amount of observation time. Table 4 shows that the high ratio value of 4.00 for the hour 6:00 A.M. to 7:00 A.M. in winter is derived from only one half-hour observation period. Similarly the ratio, 4.34, for 8:00 A.M. to 9:00 A.M. is obtained from only six half-hour periods. These two ratio values would be much more reliable if they were derived from considerably more observation time. The most misleading ratio for spring data is that for the hour between 7:00 P.M. and 8:00 P.M. This very high ratio of 5.00 is substantiated by only one hour of observation time, and is most likely the result of insufficient sampling. Summer data contain a 3.14 ratio for 6:00 A.M. to 7:00 A.M. Although this value is not

unduly high to conform to the diurnal activity pattern, it should be interpreted cautiously because it is supported by insufficient observation time. Also, the ratios from 10:00 A.M. to 11:00 A.M., 11:00 A.M. to 12:00 M., and 12:00 M. to 1:00 P.M. fall into this category, although they represent neither extremely great nor small amounts of activity. Autumn data contain several ratios which would be more reliable if they were supported by additional observation time. As they are, they conform to the activity pattern; nevertheless, four, nine, seven and two observation periods are insufficient to be completely trustworthy when compared with the amount of observation time for other hourly periods.

In autumn, squirrels appear to be more active from 11:00 A.M. to 12:00 M. than at any other time. The majority of squirrels seen at this time were foraging on the ground in the near vicinity of oaks, butternuts and black walnuts. From 12:00 M. to 2:00 P.M. is an active time during winter. It is possible that temperature is a contributing factor to increased activity during this two-hour period, because the highest temperature of a winter day often occurs at this time.

A general comparison of physical environmental factors by Chapman (1931) established the relative importance of temperature. It often conditions the reactions of an animal to other stimuli. Merriam (1884) stated that the red squirrel remained active throughout the continuance of excessive cold. Hatt (1929) noticed that severely cold weather caused the red squirrel to become inactive. According to Dice (1921) very few red squirrels in Alaska were active when the temperature dropped below minus 30°F. Seton (1929) stated that he often saw red squirrels active at temperatures of minus 20, 30 and 35°F. From census studies of the red squirrel Hamilton (1939) concluded that prolonged periods of cold might cause squirrels to remain holed up, but that inclement weather during a mild season exhibited little effect on their activity. Allen (1942) cited the instance wherein two female fox squirrels in or approaching a period of oestrus were known to have been inactive during cold weather for two or three days. From this he concluded that the sexual urge might not conspicuously modify a tendency for them to remain in their nests during periods of extreme weather. Brown & Yeager (1945) found that both gray and fox squirrels in Illinois were active throughout the year but exhibited least activity during periods of unusually cold weather. Heat as well as cold appeared to reduce animal activity.

Data accruing from this investigation indicate that the fox squirrel is active in all temperatures of natural environment. However, on several occasions when temperatures were at 90°F and above, the fox squirrel displayed unmistakable lethargy. Its movements were relatively slow and deliberate, and it appeared inclined to exert itself as little as possible. This substantiates the findings of Brown & Yeager (1945). At high temperatures the fox squirrel commonly stretches out on a limb and remains passive during

the heat of the day. Extremely low temperatures by themselves do not retard squirrel activity as much as do high temperatures. However, low temperatures associated with other meteorological factors such as high wind, complete overcast or driving snow restrict movement very noticeably.

The interaction of seasonal influence and temperature should not be disregarded. Temperatures conducive to the greatest amount of activity—lie between 40°F and 49°F. This well-defined peak of activity is probably bolstered by autumn temperatures which often fall within this bracket, and autumn is the season in which most activity occurs largely as a result of foraging and food storing activities. Evidence that fox squirrel activity is not dependent solely upon temperature fluctuations is presented in figures 1, 2, 3, and 4. In several instances consecutive mean hourly temperatures of approximately equal value are not accompanied by respective similar amounts of activity.

Daily and seasonal fluctuations in humidity profoundly affect the behavior of animals. An example of the interaction of humidity and temperature was presented by Pearse (1939) who stated that large homeothermic animals commonly evaporate water from their external or internal surfaces to cool their bodies, and suffer discomfort in high temperatures and humidities.

Generally speaking, relative humidity is inversely proportional to temperature. Observations made in early morning before sunrise are usually accompanied by relatively high humidities and low temperatures. Most of the observations made in July, 1946, were by linear method. Those made in early morning almost invariably had high humidities. These readings are direct cause of the noticeable increase for linear count from humidities of 90 to 100% in Table 6. The high relative humidities for spot count are mostly a consolidation of readings taken during full daylight hours but caused by recent precipitation, and are independent of time of day. Thus, one realizes that it is incorrect to say that fox squirrels will be most active at a certain humidity. They tend to be most active in late morning and early forenoon when humidities are often relatively high. In this instance an analysis of the modifying factors indicates that time of day and temperature as well as humidity are important influences controlling squirrel activity. During other hours of the day though, when high humidities are caused by precipitation, one realizes that wind velocity and precipitation interacting with humidity combine to lessen the amount of activity.

Whether the fox squirrel is discomforted by the effects of humidity is not known. Consequently, we do not know to what extent relative humidity *per se* modifies squirrel activity. This investigation reveals that the fox squirrel is more active at relative humidities between 50 and 59%. However, the writer believes that humidity alone is not responsible for this fact. Instead, the humidities contained within the 90 to 100% group are those which most frequently interact with other environmental factors most conducive to a relatively greater amount of squirrel activity.

This analysis can be carried farther by considering the comparatively small amount of activity occurring at relative humidities from 20 to 39%. Most of the observations made at these humidities were on summer days in the afternoon when activity is relatively low. Most of the days possessing such low humidity readings had high temperatures ranging from 80°F to 99°F. These days were characterized by relatively high wind velocities grouped mostly between seven and nine miles per hour. Regardless of whether or not lack of sufficient moisture in the air causes the fox squirrel to become less active, it is certain that the other ecological factors just mentioned influence activity simultaneously.

Wind movement is considered by several writers as one of the most important weather factors influencing the fox squirrel's activities. Baker (1944), Goodrum (1937), Brown & Yeager (1945) and Seton (1929) mention the effect of wind on squirrel movement. In general, the amount of activity is inversely proportional to wind velocity. This is especially true of squirrel movement in trees. A high wind sways and tosses small branches and renders a squirrel less sure of its footing. Under such a condition it is difficult for a squirrel to measure its jumps. The force of a strong wind against a squirrel's body and especially against its tail increases the animal's difficulty in maintaining balance while it is in the process of leaping and when it is traversing small branches. A high wind does not restrict squirrel activity on the ground as much as it restricts movement in trees.

Spot count data indicate minimum squirrel activity in wind velocities exceeding 10 miles per hour (Table 7). However, linear count data reveal exceptionally high activity at velocities of 11 and 15 miles per hour. These velocities for both spot and linear counts are not substantiated by sufficient observation periods to warrant a superficial interpretation. Four squirrels in two observation periods were seen in an 11 miles an hour wind. Five squirrels in two observation periods were seen in a 15 mile an hour wind. The degree of activity in these two velocities is much greater than would ordinarily be expected. Probably seasonal influence is the chief reason for the pronounced activity during the 11 miles an hour wind. The observation was made in November when squirrels were very active storing nuts. Most of their activity was confined to the ground rather than to trees. The cause of the exceptional activity during the 15 mile an hour wind is unknown. Several other concurrent ecological factors were also of such nature as to ordinarily curtail activity. The observation was made on a clear day in January from 11:30 A.M. to 12:30 P.M. at a temperature of 9°F and relative humidity of 60%. There was one inch of snow on the ground.

It is difficult to ascertain the effect of wind currents upon fox squirrel activity. Primarily, the wind velocity value itself is a somewhat arbitrary figure.

Wind velocities increase with vertical distance from the ground. An anemometer at ground level may indicate a wind velocity of two miles per hour. At a height of six feet it may record a six mile an hour wind. At tree top height the velocity might be 15 or 30 miles per hour. Wind velocity readings used in this investigation are based upon averages obtained from readings taken at ground level and at five feet from the ground. Consequently, the ultimate values used are relatively low because velocities at tree top level are not contained in the averages. The influence of topography upon evaluation of data contributes an additional problem. Wind velocities are much less in ravines and sheltered areas than on ridges and relatively open stretches of floodplain. Squirrels may be quite active in ravines but may avoid exposed areas subject to the full force of the wind.

Changes in atmospheric pressure exercise certain influences upon mammalian behavior. This is readily evident to an exaggerated degree in abrupt increases in altitude. Chapman (1931) stated that most investigations seem to show metabolism in general is affected by the action of pressure upon the gases involved in respiration. It is difficult to differentiate between the influences of atmospheric pressure as such and the effects it has upon other factors. Hamilton (1939) observed that both red and gray squirrels in New York were noticeably active prior to a snow storm. The red squirrels appeared to be very excited and raced about gathering in food supplies. Such action might possibly be attributable to the influences of falling atmospheric pressure and other meteorological factors. Table 8 indicates that fox squirrel activity increases slightly with an increase in barometric pressure from 29.60 inches to 30.49 inches. It is doubtful that increased activity is a reflection of the influence of pressure alone. Greater activity is more likely the result of a combination of weather factors which are progressively more conducive to squirrel activity as barometric pressure increases. For example, fair days are more common in a high pressure area than in a low pressure area.

The fox squirrel does not appear to be as sensitive to the variations between a partly cloudy and a clear day as it is to the differences between a cloudy and a partly cloudy day. Complete absence of sunshine decreases squirrel activity. Partial sunshine, if only for a brief portion of an observation period. stimulates activity.

Precipitation can affect the activity of an animal in several ways. If an animal preferred an individual condition of dryness to wetness, then the purely physical properties of rain and melting snow would be sufficient to cause discomfort. The physical impact (relationship to wind velocity) of rain, snow or hail might in itself cause animals to seek shelter and remain comparatively inactive. Specifically, the temperature of a gentle rain might be so low that it, rather than the rain itself, would cause a decrease in activity. Baker (1944) noticed that Texas tree squirrels were less active following a rain. From

observations made by Allen (1942) on the fox squirrel in Michigan, rain appeared to be no deterrent to activity if the weather was warm. Brown & Yeager (1945) noticed that both the gray and fox squirrels were less active on rainy days. It appears that slight or moderate precipitation, especially snow, does not retard squirrel activity as much as does a high wind. Several times squirrels were seen foraging during a snowfall or a light rain. Data from combined counts indicate that the fox squirrel is more active in snowfall than in rain. Possibly snow does not wet the pelage as quickly as does rain. A blizzard, however, definitely retards activity. In such weather, decreased activity appears to be a negative response to high wind velocity rather than to low temperature. Probably the physical impact of driving snow is a contributing factor in causing the animal to seek shelter. In either rain or snow the element of overcast should not be disregarded as one of the factors which decreases activity.

No effects of thunder or lightning upon squirrel activity were observed, in spite of the fact that observations during thunder and lightning were not uncommon.

Several factors accompanying snow depth contribute to a modification of animal activity. Texture of the snow affects animal movement. Deep fluffy snow renders movement of the relatively smaller mammals more difficult than does a deep crusted snow. Texture and depth are important factors in determining the ease of successful foraging for food. Observations by Allen (1942) indicated that fox squirrel activity in the winter appeared to be conditioned by temperature and snow depth. Fox squirrels were seen foraging when snow was eight inches deep according to Brown & Yeager (1945).

In this investigation more complete data were obtained by linear count at various snow depths than by spot count. Nevertheless, additional observation time is needed for both methods in order that more reliable information be obtained. Linear data indicate that squirrels are more active when patches of snow are present than when the ground is bare of snow. The two conditions are probably irrelevant as causes of this variation of activity. The primary cause is most likely a seasonal influence such as food supply. Data from both count methods show that activity is definitely decreased by increased snow depth. All observations concerned with depth of snow include only a fluffy snow. No observations were made when snow was crusted and packed hard. The processes of squirrel movement are impeded by snow five inches or more in depth. Locomotion is by bounding. The deeper the snow, the more exaggerated is the bound vertically. Foraging is made difficult because the animal is unable to use its slow, exploratory walk or gait.

Throughout this section and the section on "Findings," it has been necessary to interpret the data by considering each ecological factor, not as a separate element to be analyzed as such, but as an environ-

mental influence the effects of which upon the fox squirrel are modified by the complicated interactions of other factors. If the plan of research were such as to attempt treating each ecological factor as a separate entity, and by such treatment to measure in detail the effects of that factor upon animal activity, then all other factors which help to shape the environment should be so controlled or selected with respect to time and place that they could be treated as a constant. This procedure appertains for each variable that is to be investigated. The complications of such a research plan increase with the number of variables to be considered. For example, if the specific effects of temperature alone are to be considered, then season, time of day, relative humidity, barometric pressure, wind velocity, overcast and all other influencing factors should be constants for all the periods during which the effects of varying temperatures are observed. It was impossible to conduct this investigation in accordance with such a detailed and exacting plan with the time and equipment available.

SUMMARY

1. The fox squirrel in Iowa displays varying degrees of activity depending upon season. Activity during autumn is noticeably greater than that in any other season, and is least during spring and summer.

2. Activity is greatest during December, followed by November, October, and January in order of intensity. Least activity occurs in July, May, June, and August.

3. The fox squirrel is diurnal. It is seldom active before sunrise or after sunset.

4. By hourly segregation, most activity occurs from 7:00 A.M. to 8:00 A.M. Lesser major peaks of activity are from 11:00 A.M. to 12:00 M. and from 6:00 A.M. to 7:00 A.M. Least daytime activity occurs between 4:00 A.M. to 5:00 A.M., 2:00 P.M. to 6:00 P.M., and 7:00 P.M. to 8:00 P.M.

5. There are three peaks of activity throughout the day. The most intense activity occurs from 6:00 A.M. to 9:00 A.M. The second peak is from 11:00 A.M. to 1:00 P.M. The third and minor peak is from 6:00 P.M. to 7:00 P.M.

6. Activity in winter is greatest from 8:00 A.M. to 9:00 A.M. and 12:00 M. to 2:00 P.M. It is least from 2:00 P.M. to 5:00 P.M.

7. Spring activity is greatest from 5:00 A.M. to 11:00 A.M. and is least from 2:00 P.M. to 4:00 P.M.

8. Greatest activity in summer occurs from 6:00 A.M. to 7:00 A.M. and from 6:00 P.M. to 7:00 P.M. Least activity occurs from 4:00 A.M. to 6:00 A.M., from 3:00 P.M. to 5:00 P.M. and from 7:00 P.M. to 8:00 P.M.

9. Activity in autumn is most intense from 6:00 A.M. to 9:00 A.M. and from 11:00 A.M. to 12:00 M. It is least from 5:00 A.M. to 6:00 A.M., 2:00 P.M. to 3:00 P.M., and from 5:00 P.M. to 6:00 P.M.

10. The fox squirrel is most active at temperatures ranging between 40 and 49°F. Temperatures at which activity is least are those from 15 to 19°F and from 75 to 84°F.

11. Greatest activity occurs at relative humidities between 50 and 59% and between 80 and 99%. Least activity occurs at relative humidities from 20 to 39%.

12. Wind velocity is one of the most influential environmental factors affecting squirrel activity. Magnitude of squirrel activity is inversely proportional to wind velocity. Activity is greatest in a wind with velocity of two miles per hour, and is least in a wind with velocity of nine miles per hour. Of all environmental influences considered, the effects of wind are least interrelated with the effects of the other factors.

13. Intensity of squirrel activity increases slightly with increases in barometric pressure, but the specific effects of pressure isolated from the interactions of any other environmental factor are unknown. Activity is greatest at pressures from 30.40 inches to 30.49 inches and from 30.10 inches to 30.29 inches at 800 feet above sea level. Least activity occurs at pressures between 29.60 inches and 29.69 inches.

14. Intensity of activity is inversely proportional to the degree of cloudiness. Least activity occurs on cloudy days. Greatest activity occurs on clear days.

15. Light rains, drizzles and mists are relatively moderate in their effects upon squirrel activity.

16. Snowfall decreases activity but to a lesser extent than does rain. Squirrels are more active at those times which have no precipitation than at those which have rain or snow.

17. Activity is affected only slightly by snow that is two inches or less deep. Snow more than two inches deep impedes activity. Snow patches have no appreciable effect upon activity.

18. The effects of each environmental factor must be interpreted only after due consideration has been given to the interrelationships of that specific factor with the other influences comprising the environment.

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SOIL-ROOT RELATIONSHIPS OF CERTAIN NATIVE GRASSES
IN VARIOUS SOIL TYPES

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SOIL-ROOT RELATIONSHIPS OF CERTAIN NATIVE GRASSES IN VARIOUS SOIL TYPES

INTRODUCTION

Knowledge of the soil as a medium for the growth of roots has increased very greatly in the past three decades. Earlier studies on the root depth and distribution of native midwestern range and pasture grasses were made with only minor consideration of specific soil types or soil horizons (Weaver 1919, 1920; Sperry 1935; Albertson 1937). The objectives of these early studies were to ascertain the general relationships of roots to soil and to each other as regards spread, depth, and degree of development in the same community and in different and widely separated units of vegetation. Some attention was given to the response of root systems to the great drought (Weaver & Albertson 1943). These studies formed a background for similar studies of crop plants (Weaver, Jean, & Crist 1922; Jean & Weaver 1924; Weaver 1926; Weaver & Bruner 1927).

With the rapid development of soil science and much emphasis on the role of vegetation, especially grasses, in soil formation, a distinct need has arisen for a better understanding of the intimate relations of roots and soil. A beginning was made by Hanson & Whitman (1938) in their study of the characteristics of major grassland types in western North Dakota. They observed the abundance and depth of roots in the several soil types. Study has been made of the quantities of organic materials provided to the soil by the mass of grass roots, and the rate at which they are formed (Weaver & Zink 1946; Weaver, Hougen, & Weldon 1935). The quantity of living underground materials, especially in the upper portion of the soil, has been ascertained (Weaver & Harmon 1935; Shively & Weaver 1939). Some information on the length of life of individual roots has been obtained (Weaver & Zink 1946a) as well as the length of time required in grassland for roots to decompose and return to the soil (Weaver 1947). The effects of grazing on the root systems of several range grasses have also been ascertained (Weaver & Darland 1947).

A new method has been devised which consists of obtaining representative samples of entire root systems, of studying the intimate relations of roots and soils, and of measuring root production quantitatively at various soil levels. This, together with more exact mapping of soils, a better understanding of the relationships of one soil type to another, and especially the greater accuracy and detail with which soil profiles are now described, makes it possible to ascertain more definite relationships between the roots of grasses and the soil in which they grow.

METHODS

The method of obtaining samples is a modification of the direct or trench method (Weaver 1926) which has been employed successfully over a period of several decades. It consists in the digging of a trench to the desired depth in a particular soil and the obtaining of a single undisturbed column or monolith of soil extending from the surface well into the "C" horizon and often of such length (3 to 5 feet) as to contain the longest roots of the native grasses in unbroken sod. The monolith should be of such dimensions that it can be removed from the trench and transported without special equipment. Particularly it should contain a representative sample of roots that are not too massive for careful separation from the soil by means of washing nor too abundant to reveal detailed distribution and density at the several soil levels.

Strong boxes without tops were made of ⅞-inch-thick planed boards of white pine. The bottom consisted of a single board a foot (actually 11.75 in.) in width and 3, 4, or 5 feet long. To this board, sides of similar material were fastened with nails and screws in such a manner that the 11.75-inch-wide box had an inside height of exactly 3 inches. One end was left open. Appropriate cleats of wood fastened to the bottom with screws effectually prevented warping and added much rigidity. The boxes were kept well painted. In use, a box was placed on end with the open end up, to contain the soil monolith which was 11.75 inches wide, 3 inches thick, and 3 to 5 feet in length.

SELECTING THE SITE

Studies were made in areas of native grassland in the eastern half of Nebraska and in northern Kansas. The histories of these prairies were well known by the writers. The prairie grasses were disturbed only by annual mowing, unless pasturing is indicated. Soil maps of the several counties were consulted and the type of soil, or its variation where samples were obtained, was carefully checked by professional soil examiners. The plan followed was to obtain monoliths within pure stands of certain species of grasses in a wide variety of soils. In all, 33 monoliths were taken with 10 species of grasses in 16 soil types.

PREPARING THE TRENCH

After a site with apparently normal development of vegetation was chosen, tarpaulins were spread on the ground by the sides of the place selected for digging. When soil was placed on these it greatly facilitated refilling the trench and reduced damage

to the vegetation. The soil-root relations were observed as far as possible, and the root depth was noted as the soil was removed. Where a single monolith was taken, a trench 3 feet wide and about 4 feet long was convenient. But where two or more monoliths were to be taken, larger trenches were excavated. The depth, which was determined largely by the root length, was usually a foot deeper than the longest roots (3 to 5 ft.) in the monolith. The side walls were kept nearly vertical, despite the directions taken by some roots, since in prairie grasses most roots usually pursue a vertically downward course.

Marking Out the Monolith

Beneath the particular sample of grass, previously selected and left undisturbed in the side wall, the wall of the trench was made smooth and vertical, as shown by a plumb line. A box was then placed on end, with the closed end downward. The open top was placed against the trench wall, the upper end just reaching the soil surface. An impression of the sides and end of the box was made on the wall of the trench by tapping the bottom of the box vigorously with a four-pound sledge hammer. The box was then removed and the soil column marked out with butchers' knives with rigid blades. Then the soil on the sides and below these marks was removed by means of knives and spades until the monolith protruded from the trench wall, the bottom and sides extending outward at least 3 inches. Next the box was fitted tightly over the monolith and the bottom and lower end of the box were braced to hold this soil mass in place. Finally the soil on the inner, attached face of the monolith was cut away by work-

ing inward with knives and spades from each side. The soil was not cut close to the top of the box, but a V-shaped ridge of soil protruded throughout its length. This was a part of the sample when the braces were removed and the monolith was lifted out of the trench. The sample was placed in a truck, covered and kept damp to avoid serious cracking, until it was taken to the laboratory for an examination of the profile. Usually several monoliths were obtained on a single field trip.

Examination of Soil

The V-shaped ridge of soil protruding from each monolith was used in an examination of the profile. A complete description included not only the depth of the main soil horizons and the subdivision of these into their minor parts, but also the color, texture, structure, consistence, and pH of each subdivision. Complete descriptions were made of nearly all of the soil types; a few were somewhat abbreviated. The examination of a soil after some drying has distinct advantages. Soil may easily be moistened to compare its characteristics in a wet condition. Correlations of soils and descriptions of the profiles were made by James Thorp, W. I. Watkins, and B. H. Williams of the Division of Soil Survey, U. S. Department of Agriculture, and the Conservation and Survey Division, University of Nebraska. The authors are deeply grateful to them for this service. A photograph showing the root distribution in each of the soil types has been submitted to be filed with the official description of the soil. The soil types are numbered consecutively in this paper to permit ready reference to them. Table 1 contains data on a soil in monoliths with three

TABLE 1. Description of a monolith sample of (1) Sharpsburg silty clay loam,[1] taken in a ravine in the ecological experimental prairie 3.5 miles northwest of the University of Nebraska in Lincoln.

Horizon	Depth	Color[2]		Texture	Structure	Consistence (moist)	pH by Soiltex
		Dry	Moist				
A$_{1-1}$	0- 7	Very dark gray 10YR 3/1	Very dark brown or black 10YR 2/1.5	Clay loam	Fine granular	Friable	6.5
A$_{1-2}$	7-12	Dark grayish brown 10YR 2.5/2	Very dark brown 10YR 2/2	Clay loam	Medium or coarse granular	Friable	6.5
B$_1$	12-18	Grayish brown 10YR 4/2	Dark grayish brown 10YR 3/2	Light[3] silty clay loam	Fine blocky	Slightly plastic	6.5
B$_2$	18-28	Brown 10YR 4/3	Dark brown 10YR 3/3	Silty clay loam	Blocky	Moderately plastic	6.5
B$_3$	28-48	Yellowish brown 10YR 5/4	Dark yellowish brown 10YR 4/4	Silt loam	Ill-defined blocky	Friable	6.5
D$_1$	48-66	Yellowish brown 10YR 5/4	Dark yellowish brown 10YR 4/4	Silt loam containing thin lenses of fine sand	Massive or somewhat stratified	Friable	6.5

[1]This soil is mapped as Carrington soil, but can be considered only as a mapping inclusion; till from which the Carrington soils were formed lies below the solum at the point where this soil was studied.
[2]Provisional Soil Survey color names, based on standard Munsell color charts; e.g., 10YR 5/2 means: hue is 10 yellow-red; value on lightness scale is 5; chroma saturation is 2. The color names are those of common usage.
[3]"Light" silty clay loam means that the soil has near the minimum of clay content for that texture class.

different species taken from the walls of one trench. To conserve space the descriptions of soils that follow are presented in paragraph form rather than in tables.

Explanation of letters representing soil horizons are as follows:

A_1 The dark upper part of the uppermost horizon. Usually high in organic matter.

A_2 The lower part of the uppermost horizon of the soil that is leached, definitely lighter colored than the A_1, and lower in organic matter.

A_3 A transitional horizon, usually with more clay than horizons above and less clay than the B horizon. Usually thin.

B_1 A transitional horizon with more clay than A. Usually thin.

B_2 A subsoil horizon with much more clay than the A horizon, and usually with much less organic matter.

B_3 A horizon transitional between the B_2 and C or parent material.

C_1, C_2, etc.   Parent material in various stages of weathering.

D   horizons are materials beneath the soil that are different from parent material.

Each of the horizons may have subdivisions: e.g., A_{1-1}, A_{1-2}, A_{2-1}, A_{2-2}, B_{2-1}, B_{2-2}, etc.

One or more horizons are missing from some soils.

PREPARING AND WASHING AWAY OF THE SOIL

Upon completion of the soil descriptions the excess soil was cut away even with the sides of the box so that the broad monolith was exactly 3 inches thick. It was then submerged in a large tank of water. Here it was soaked for a period of 2 to 5 days, depending upon soil type. Sometimes after the soil in the top of the box had been washed away the remainder was again soaked; then further washed, and soaked again. In washing, the box was placed at an angle of 10 degrees, the tops of the plants always being highest.

A flaring rose nozzle attached to a garden hose was employed. It spread the water uniformly through 107 small apertures and thus reduced the pressure of the water on the roots in any one place. The amount of water pressure used varied with the soil type and with the horizons in the same type. Too much pressure can easily ruin the root system. The rule was to use just enough pressure to gently remove the soil. The writers nearly always worked together in washing. Often it was necessary to wash the soil away under water and even then the more delicate roots had to be protected by the hand. All the soil removed was caught on a series of screens of 15 meshes per inch. Only a very few loose roots, usually a small fraction of 1 percent by weight, were found on the screen. These were roots that had entered the monolith from the side and did not intertwine with the main root mass sufficiently to be held in place. In fact, it was not the loss of roots but keeping the root pattern undisturbed that required the most careful attention.

The examination of soil-root relations under a shallow layer of water while washing reveals many features since the soil is slowly removed and new soil constantly comes into view. An exposed main root may be followed easily throughout its entire length, the branching being clearly revealed, and some of the details of soil-root relations examined.

Where the soil of the C horizon was easily removed but that of the B horizon was very compact, it was sometimes necessary completely to remove the A horizon by washing, then the refractory B layer, leaving the roots in the C horizon protected by the soil until this had been accomplished. Otherwise they would have been injured by the overflow of soil and water. Sometimes the granules in a blocky soil structure could be removed more easily by carefully loosening them with an ice pick. Efficiency and success were gained only by experience. But one felt well repaid for the time spent when after 3 to 5 hours the complete root system alone was left in almost perfect condition in the bottom of the box.

PREPARING THE ROOTS FOR PHOTOGRAPHING AND QUANTITATIVE STUDY

The network of roots was placed on a large, smooth, painted board which was kept wet and tilted at an angle of 10 degrees. One end of the board was placed in a sink. A thin sheet of water was kept flowing over the board continuously while any tangled roots were separated by means of dissecting needles and a hand spray. They separated readily and assumed their natural position only as long as they were kept under water. Sometimes this was accomplished by placing a weighted board in the bottom of a shallow tank of water and letting the roots spread into their normal position and then slowly siphoning off the water until the root system lay spread out on the board. In a few instances where there were tangled root fragments, it was necessary to float them in a separate container of water and then replace them in position on the root system. Of course, much time was saved by keeping the roots from getting tangled as the soil was removed by a proper system of washing.

All excess water was removed by means of blotters from the roots and the board. The roots were then covered with moist newspapers. At this stage and in this condition they could be kept for several days. A mounting board of light plywood, covered with black felt securely tacked in place, was inverted and placed over the root system after the newspapers were removed. The two boards were held firmly together while they were inverted. The end of the painted board near the top of the root system was then raised slightly. Usually the roots did not adhere to this board but lay on the black felt. If they did adhere they were loosened by using the smooth edge of a yardstick. After removal of the top board the roots were covered with damp paper and pressed firmly with the hand onto the felt. The crown was anchored by means of a few small nails driven into the mounting board. Then the entire mount was placed in a vertical position for photographing.

PHOTOGRAPHING AND SECTIONING THE ROOT SYSTEM

Photographs were made by the University of Nebraska Photographic Laboratory. The lighting was done by electro-flash units, one unit being placed
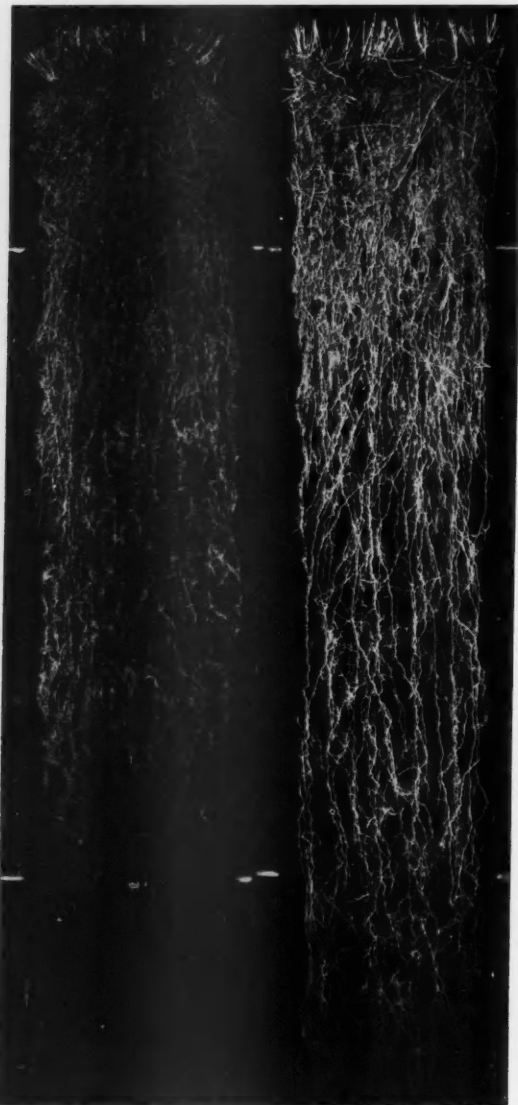

FIG. 1. Root system of little bluestem (*Andropogon scoparius*) at left, and switchgrass (*Panicum virgatum*) at right, taken from 5-foot monoliths with soil profile as shown in Table 1. The shallower rooted bluestem (about 5 feet) has a greater concentration of materials in the A horizon (0-12 in., above upper lines) than the 10-foot-deep switchgrass. But bluestem has only 38 percent as much root-weight as switchgrass in the B horizon (12-48 in., between the lines). In this and following figures, the width of the root system is 12 inches.

on each side of the camera. The writers are greatly indebted to Mr. W. Hoffman and to others of his staff for this excellent service (Fig 1).

The root system was then sectioned in such a manner that the oven-dry weight at 100°C. could be ascertained for each 6-inch or foot depth and also for each of the major soil horizons. For example, where the A horizon was between 0 and 7 inches and the B between 7 and 22 inches, the root system was cut and weighed as follows: 0-6 inches, 6-7, 7-12, 12-22, 22-24, and 24-36 inches. In this work the underground materials in the surface 6 inches, whether roots, rhizomes, or stem-bases, are designated as roots. No attempt was made to separate roots from other plant materials.

In concluding the description of the method, the writers wish to state that it may seem long, tedious, and laborious. This we acknowledge. It must be judged solely by the results obtained.

EXAMPLES OF ROOT DISTRIBUTION IN DIFFERENT TYPES OF SOIL

The root distribution of three species of grasses in three different soil types near Lincoln, Nebraska, will be used first to illustrate some soil-root relationships. These were among the first of the 33 monoliths examined. The grasses are Kentucky bluegrass (*Poa pratensis*), blue grama (*Bouteloua gracilis*), and big bluestem (*Andropogon furcatus*)[1]

One group of monoliths was taken from an upland pasture adjoining Pioneer Park on the west and a second (except for blue grama) in an adjacent lowland. The third lot was taken from lowland in the ecological experimental prairie 3.5 miles northwest of the University of Nebraska.

The first monoliths were from Carrington silty clay loam. It is an old soil developed on glacial drift before the Peorian loess was deposited upon it. The A horizon is shallow (0-7 in.). The soil had been trampled by stock, and there was much compaction. Penetration of water was poor. The third foot in the reddish, clayey subsoil, except the upper two inches, was filled loosely with rock and pebbles from 2 inches to $\frac{1}{16}$-inch in diameter. Below 3 feet the hard, dry, pebble-filled soil was difficult to remove even with a hand pick.

2. CARRINGTON SILTY CLAY LOAM

Hori-zon	Depth in.	Description
A₁	0- 7	Very dark grayish brown (10YR 3/2 dry) heavy silty clay loam; granular; pH 5.5
B₁	7-10	Dark grayish brown (10YR 4/2 dry) heavy silty clay; granular; pH 5.9
B₂	10-22	Brown (10YR 4/3 dry) clay; coarse granular or fine nuciform; pH 6.1
C and D	22-36	Dark yellowish brown (10YR 4/4 to 10YR 5/4 dry) clay; blocky; pH 6.9; no free lime

The monoliths were taken on the nearly level hilltop. Each kind of grass grew in locally pure stands. The two shorter grasses had been subjected to graz-

[1] Nomenclature of the grasses is according to Hitchcock's "Manual of the Grasses of the United States."

ing, but big bluestem in a closely adjacent area had been protected from grazing.

The second excavations were made in a large, lightly grazed pasture at the foot of the hill and only a quarter of a mile distant. They were in Wabash silty clay loam. This is a young alluvial Wiesenboden (moist meadow) soil with only slight development of the profile. Changes are gradual with increase in depth.

3. WABASH SILTY CLAY LOAM

Hori- zon	Depth in.	Description
A	0-13	Black (10YR 2/1 moist) silty clay loam; fine granular; pH 7.4
B_1	13-27	Black (10YR 2/1 moist) silty clay; granular; pH 7.5
B_2	27-36	Very dark gray (10YR 3/1 moist) clay; coarse granular; pH 7.6

This soil had much fine material from deposits of calcareous loess which had been washed in from the upland. A weak columnar structure was found at depths of 26 to 36 inches. Nutlike blocks of soil usually 0.25 to 1 inch in the long axis, but often larger, occurred. The main cracks were vertical and often 12 to 14 inches long. This soil was moist throughout and was removed with little difficulty to a depth of 5 feet where it became wet.

A third lot of monoliths was taken from a well drained lowland in the experimental prairie in Judson silt loam. The native vegetation was not disturbed except by annual mowing in fall. The A horizon of the granular silt loam is 20 inches deep. While it is a fairly "heavy" soil, a trench was dug to 5 feet in depth with no unusual difficulty. The soil is developed in silty colluvium and perhaps loess in the lower layers. It lies between the Sharpsburg soils developed from loess of the uplands, and Wabash soils of the alluvial bottomlands.

4. JUDSON SILT LOAM

Hori- zon	Depth in.	Description
Dust Deposit	0- 3	Dark gray (dry) to very dark gray (10YR 3/1 moist) silt loam; crumbs
A_{1-1}	0-11	Dark gray (dry) to very dark gray (10YR 3/1 moist) silt loam; granular
A_{1-2}	11-20	Dark gray (dry) to very dark gray (10YR 3/1 moist) light silty clay loam; granular
B_1	20-31	Very dark gray (10YR 3/1 moist) silty clay loam; granular. A few brown mottlings began at 20 inches and graded to yellow below 55 inches
B_2	31-43	Dark gray (10YR 4/1 moist) silty clay; granular
B_3	43-53	Gray (dry) to very dark gray (10YR 3/1 moist) silty clay; blocky
C_1	53-60	Light gray (10YR 6/1 dry) to dark gray (10 YR 4/1 moist) silty clay loam; blocky

The soil is slightly acid to neutral in reaction.

KENTUCKY BLUEGRASS

In the Carrington silty clay loam, the root system of *Poa pratensis* was only 22 inches deep. The bulk of the roots was confined to the shallow A horizon, 7 inches in thickness. Although roots were still abundant in the 3-inch transitional B_1 horizon, at greater depths they became noticeably less dense (Fig. 2). In the upper 3 inches of soil many of the
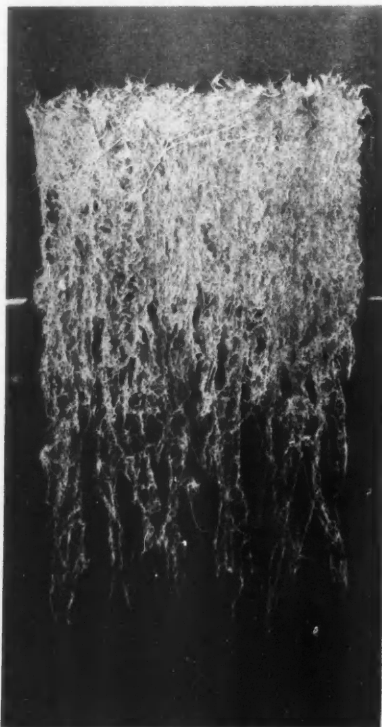

FIG. 2. Root system of Kentucky bluegrass *(Poa pratensis)* in Carrington silty clay loam. About 82 percent of the weight of roots was found in the upper 7 inches. The lines indicate this 7-inch depth of the A horizon. No roots penetrated into the C horizon which lay below the 22-inch level.

main roots spread laterally, or somewhat diagonally downward, and with the vertical ones they formed a felted mat. At greater depths most of the roots extended nearly vertically downward. A part of the shallowness of this root system may have been due to grazing and reduced vigor (Weaver & Darland 1947) but undoubtedly the type of soil was a major factor.

Roots of bluegrass in the Wabash silty clay loam penetrated much deeper, some to 3 feet. The massive portion of the root system was slightly less dense, but it extended more deeply. Ninety-two percent of the roots' weight was in the A horizon which occupied the upper 13 inches of soil. Nearly all of the roots pursued an almost vertically downward course from their place of origin, quite in contrast to those in Carrington silty clay loam. There the lateral branches were far more numerous, usually longer, and much more branched than those in figure 3.

Roots of bluegrass in the deep Judson silt loam were better developed than either of the preceding. The deep A horizon (0 to 20 inches) was well filled with a great mass of roots. But here, as in the preceding samples, they became much sparser in the B horizon. Some extremely well branched roots extended
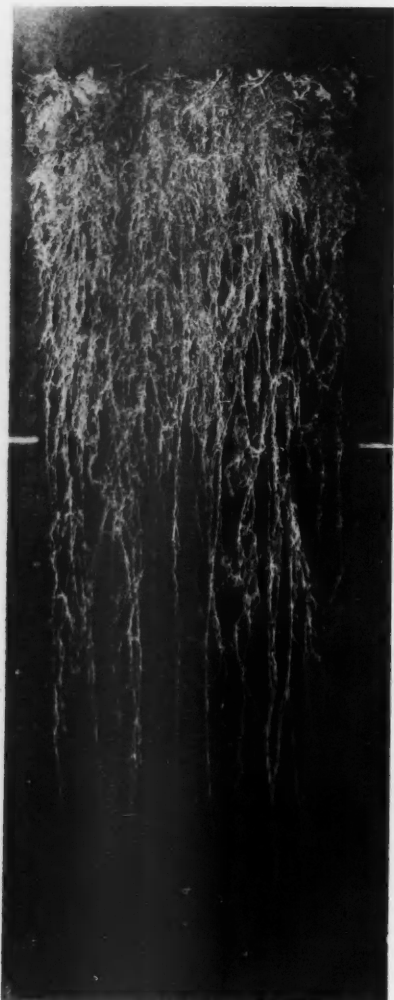
FIG. 3. Root system of Kentucky bluegrass in Wabash silty clay loam. The A horizon (above the lines at 13 inches depth) contains 92 percent of the roots by weight. The deepest roots ended in the B horizon (13-36 in.).
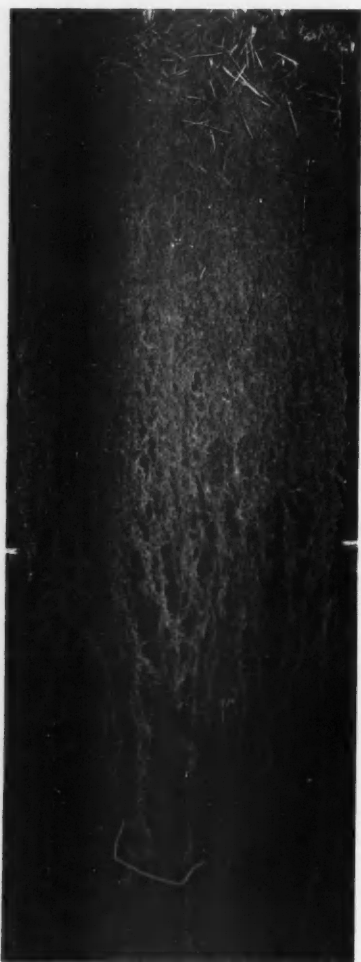
FIG. 4. Rhizomes and roots of Kentucky bluegrass in a deep, moist, but well drained Judson silt loam. The lines at 20 inches depth indicate the top of the B horizon in which the number of roots greatly decreased. Total root depth was 48 inches.

to 4 feet and ended deep in the B horizon (Fig. 4). While total oven-dry weight of the first two root systems was nearly the same, weight of the third was more than three times as great.

BLUE GRAMA

Roots of *Bouteloua gracilis* were taken in a monolith from the same trench in Carrington silty clay loam as that used in obtaining *Poa pratensis*. A photograph of the monolith was taken when about half of the soil had been removed and many of the roots were exposed (Fig. 5). Even casual examination shows clearly that the bulk of the roots are in the surface soil; actually 89 percent occurred in the 7-inch A horizon. Here they formed a dense mat of

crisscrossing threads. Roots were fairly numerous in the upper part of the B horizon. Only a few reached a depth of 3 feet where they ended in the pavementlike compacted pebbles and soil.

No blue grama grew in the second site, but numerous well developed patches occurred in the Judson silt loam. Here they had become established during the great drought (Weaver & Hansen 1941). The patches alternated with those of big bluestem and Kentucky bluegrass. The grass had flourished during a postdrought period of several years. Here again, the massive portion of the root system occurred in the deep A horizon (above 20 inches), although the transitional B1 horizon (20-31 in.) was also fairly well occupied (Fig. 6). This root system was more than three times heavier than the preceding.
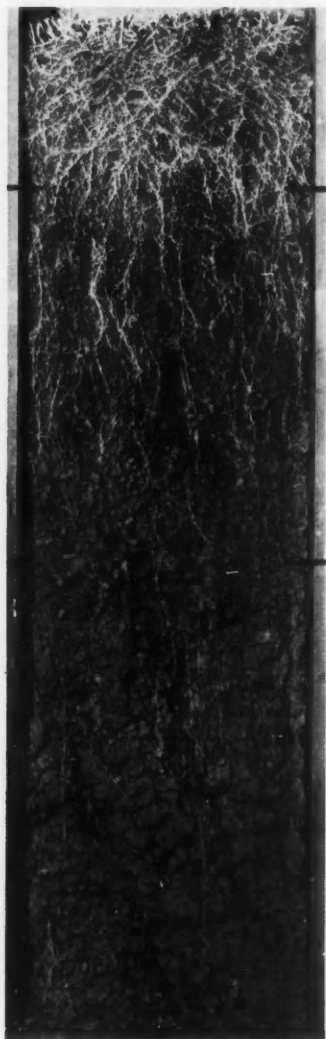
FIG. 5. A three-foot monolith of Carrington silty clay loam from which enough soil has been removed to reveal the roots of blue grama *(Bouteloua gracilis)*. There is a close correlation, as in Kentucky bluegrass, between root distribution and the shallow A horizon.

BIG BLUESTEM

The monolith of *Andropogon furcatus* was taken only about 50 feet distant from the trench on the level hilltop where the other grasses were excavated in Carrington silty clay loam. The soil was more moist than in the preceding site, in part because of a better cover of mulch and vegetation, but also because of more rapid water infiltration under big bluestem than under most other species (Weaver 1942; Weaver & Albertson 1943). Since this species is usually more deeply rooted also, it was not surprising to find a good distribution of roots in the third foot of
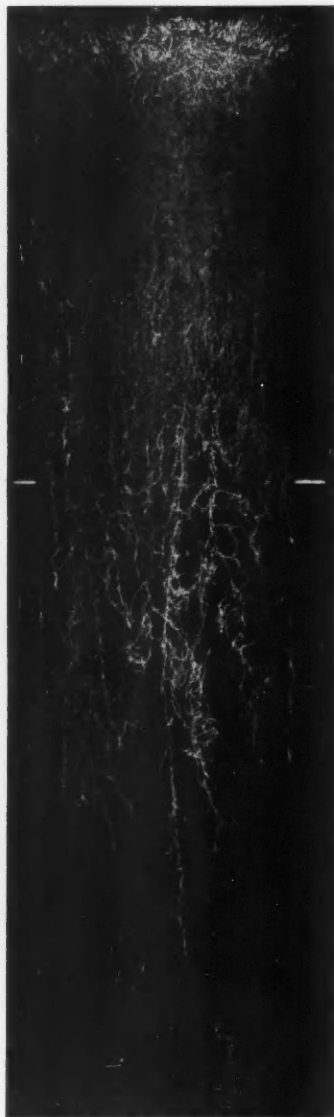
FIG. 6. Roots of blue grama from a 4-foot monolith of Judson silt loam. About 97 percent of the roots were in the upper 20 inches (A horizon, indicated by lines). Only one or two roots reached a depth of 4 feet.

soil. A few extended even deeper. That the bulk of the underground parts is confined to the upper 7 inches of soil (A horizon) may be seen in figure 7. Two striking characteristics were the fineness of the main roots and the high degree of branching.

In the Wabash silty clay loam of the lowland a great mass of roots occupied the A horizon. This lay between 0 and 13 inches depth in this trench, which was a few yards distant from the one in which Kentucky bluegrass was obtained. Roots were fewer in

Fig. 7. Roots of big bluestem *(Andropogon furcatus)* from a 3-foot monolith of Carrington silty clay loam. Decrease in the root mass below the A horizon (0-7 in.) seems less marked than in Kentucky bluegrass and blue grama. Actually 78 percent of the root-weight is in the A horizon and only 18 percent in the B (7-22 in.).

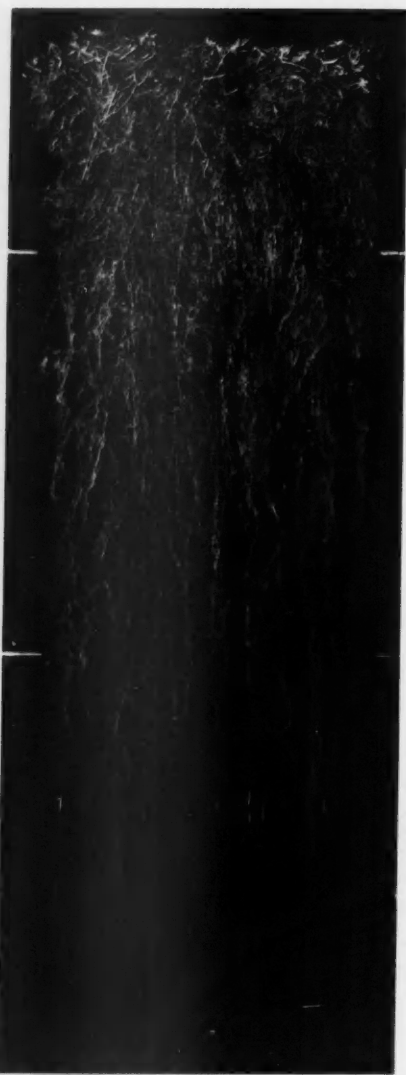Fig. 8. About 4 feet of the roots of big bluestem in a 5-foot monolith of Judson silt loam. Note the dense mat of roots in the upper 20 inches or A horizon above the horizontal lines. This mat diminished slowly in the deeper soil. Some roots penetrated beyond a depth of 5 feet.

the B horizon. Below 26 inches, where vertical cleavage occurred, the main roots followed the cracks downward, often to a depth greater than 3 feet. During washing, after the soil became very wet, the nutlike blocks (1 to 0.25 inch in the long axis) were easily separated. The branch roots were found almost entirely between these and only a few of the smallest roots ended in them.

Chief differences between the two samples were a denser mat of roots in the A horizon in the Carrington

silty clay loam than in Wabash silty clay loam. Many of the main roots were only 0.25 mm. in diameter in the Carrington but 0.5 mm. in the Wabash soil. Similar differences were found when the largest main roots were compared. The greater degree of branching of the roots in the Carrington soil was equally as pronounced as in Kentucky bluegrass. Although

these differences were very marked, especially the greater penetration of the mass of roots to more than twice the depth in Wabash soil than in Carrington, yet the total dry weight was nearly the same in both sites.

The root system of big bluestem from the Judson silt loam, and from the same trench as the bluegrass, was far better developed than either of the preceding samples. The A horizon here was 20 inches deep. It contained an immense mass of heavy, thick roots (Fig. 8). This alone weighed approximately twice that of the entire root system of either of the other plants. As usual at greater depths, the number of roots and the amount of root materials decreased rapidly. But some main roots extended to 5 feet in this very deep, fertile, but moderately moist soil.

ROOT DISTRIBUTION IN SOILS WITH CLAYPANS

"One or more groups of soils within each soil zone have peculiar properties that set them apart from soils considered 'normal' for that zone. Usually one or more horizons of each of these zones is overdeveloped and in marked contrast to the normal soil. These are called intrazonal (within-zone) soils. Planosols of the Prairie and Chernozem soil zones, and claypan soils of drier regions are intrazonal soils characterized by grassy vegetation. The most extremely developed of the Planosols have very thin surface horizons of dark-colored material rich in organic matter. Beneath the thin dark horizon is light-colored, friable, platy material several inches thick, with little organic matter, and usually moderately to strongly acid in reaction. Beneath is a strongly developed clayey horizon, or claypan" (Thorp 1948).

WESTERN WHEAT GRASS IN (5) CRETE SILTY CLAY LOAM

The first monolith from soil with a claypan was taken from a hillside in Crete silty clay loam. It was located on a midslope in a pasture adjoining the experimental prairie 3.5 miles northwest of the University of Nebraska. The pasture had been lightly grazed for several years and the western wheat grass (*Agropyron smithii*) presented an excellent, uniform stand about 18 inches high and free from other vegetation. This species had been in complete possession of the site since about 1937.

The roots had three very different habitats. The first consisted of 12 inches of a black, well granulated silty clay loam which composed the A horizon. This included nearly two inches of topsoil blown from an upland field during the drought. It was finely granulated and slightly platy in structure. The soil beneath was mellow and composed of small granules mostly 1 to 4 mm. in diameter. The granules became larger with depth and at 10 inches they ranged in diameter from 1 to 8 mm. The pH was 6.8.

At 12 inches depth there was a very distinct and abrupt transition to a blocky prismatic structure with a pH of 6.6. The clay content increased rapidly with depth and the soil was extremely hard when dry.

FIG. 9. Root system of western wheat grass (*Agropyron smithii*) in the A and B horizons from the upper 28 inches of a 4-foot monolith from Crete silty clay loam. Note the thinning of the root-mat at about 12 inches depth (horizontal lines) where it enters the B horizon. The dry weight of roots in the B horizon is less than a third of that in the layer above.

Vertical prisms varied in diameter from 3 to 4 inches; they were often 5- or 6-sided, and 8 to 12 inches long. They were sometimes broken by more or less horizontal cracks. In excavating the trench this clayey layer was removed only after much labor.

At a depth of 28 inches, the dark brown subsoil gave way to the C horizon of yellowish loess which is a silty clay loam with massive structure. It had a
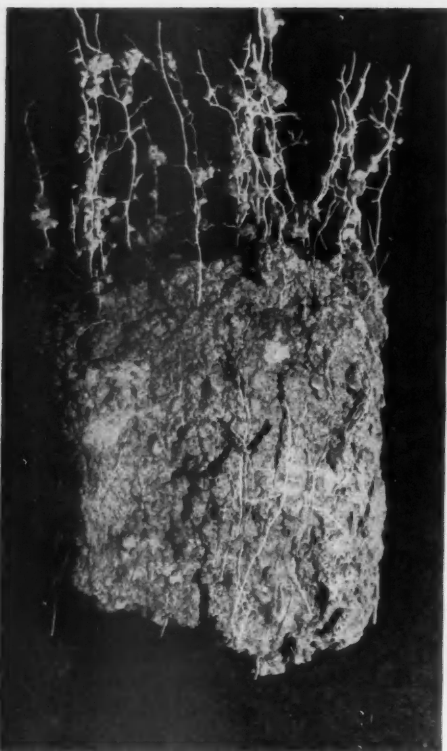
FIG. 10. Portion of a soil prism, about 3 inches in width, from the upper part of the B horizon. Its high clay content results in its being very compact when water content is low. Note the granules of soil clinging to the roots in the A horizon. The roots stretch considerably before breaking when the soil shrinks and cracks during dry weather.
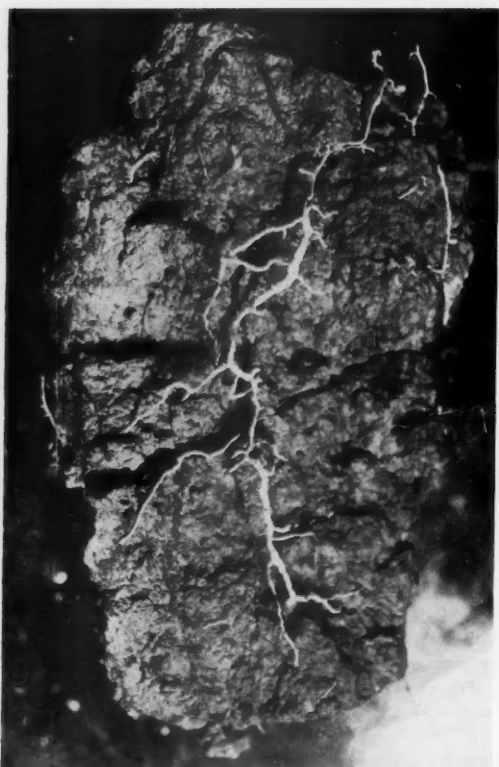

FIG. 11. Portion of a prism of soil about natural size from the lower third of the B horizon. Note the blocky structure. Many main roots grew downward on the surfaces of the prisms and were attached to the soil only by their finer branches.

much smaller content of clay. This, with the presence of abundant lime, often in small concretions, made digging much less difficult. The pH was 7.5. The soil broke up into blocky pieces to a depth of more than 4 feet.

In separating the roots from the soil it was observed that the rhizomes were confined mostly to the first two inches of topsoil. From them and from the base of the plants the tough roots, usually a millimeter or less in diameter, penetrated mostly vertically downward. They occurred in large numbers. There were about 515 at a depth of 2 inches in the 36-square-inch cross-section of the monolith. In the mellow soil of the A horizon (0-12 in.) the roots were found in great masses. They were distinctly fewer in the B horizon (12-28 in.). Only about 165 main roots entered this layer and the number decreased to 85 at two feet in depth (Figs. 9 and 10). Branching of the main roots was much less pronounced in the B than in the A horizon. While the roots penetrated this compact soil vertically through the columns (probably when they were quite moist), they were also common in the

crevices between them. Here they branched abundantly but mostly in a single plane (Fig. 11). Bundles of 3 or more living roots were often found following previous root channels.

In the mellow, moist, loessal parent material of the C horizon there was a type of root distribution distinctly different from that in the A and B horizons. The roots were often flattened on the faces of the small blocks which cleaved in all directions (Fig. 12). Thus, branching occurred in all planes. Although roots were more abundant on the outside of the cloddy masses, many were penetrated by some roots. When this moist, soft loess was washed from the roots, there remained a glistening white mass of material with branches running out at all angles (Fig. 13). Thus, the rooting habits in the three soil horizons were as different as the environment each presented. Some main roots penetrated to greater depths than 48 inches. The weight of the roots in the B horizon (12-28 in.) was only slightly greater than that part of the root system in the portion of the C horizon (28-48 in.) contained in the monolith.
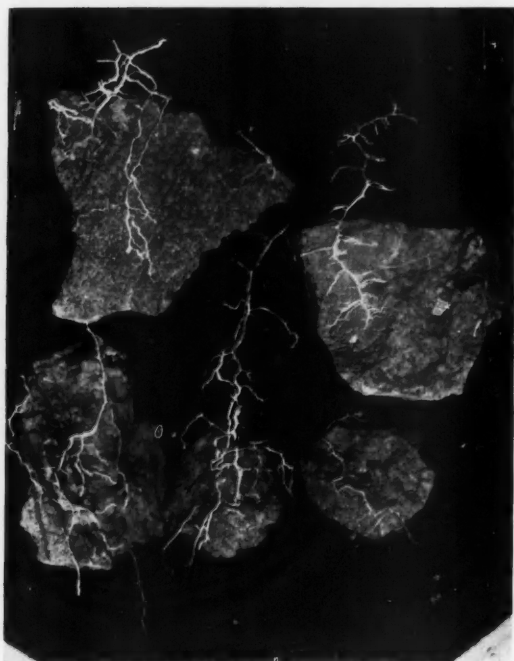
FIG. 12. Details of root patterns about natural size in the C horizon showing root branching and flattened roots on the platy lumps. Many roots scarcely entered the soil but were compressed and flattened between the lumps of parent material. Portions of roots 2 or more inches long but unattached to the soil were quite abundant.
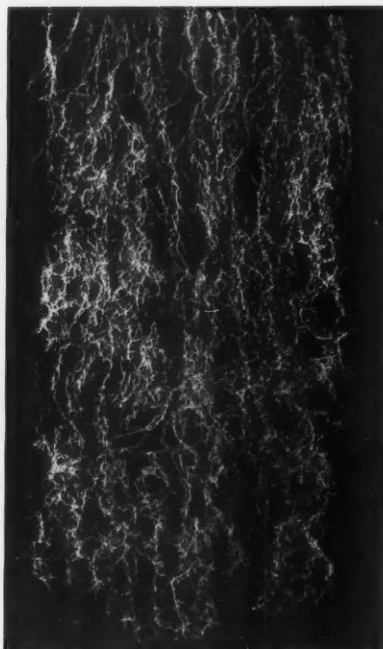

FIG. 13. Main roots of western wheat grass (about 45 in number) and their branches from the upper 20 inches (28 to 48 in. depth) of the C horizon of (5) Crete silty clay loam. This is a portion of the root system shown in figure 9.

WESTERN WHEAT GRASS IN (6) BUTLER SILT LOAM

A second monolith was taken from a claypan soil (Planosol) near Carleton, Nebraska, 65 miles southwest of Lincoln. Here the mean annual precipitation is an inch less (26.9) than that at Lincoln. The sample was from a small area of Butler silt loam, the surrounding soil type on this nearly level land being Crete silt loam. The area examined was formerly covered with bluestem grasses. But these were entirely replaced during the drought by a good stand of western wheat grass (Weaver 1943).

6. BUTLER SILT LOAM, THIN SURFACE-SOIL PHASE

This soil has a thinner A horizon than is typical of the Butler soils, and the A_2 (6 to 7.5 inches) has a little more clay than is typical for this horizon. The A_2 has an indistinct, leached, gray sprinkling of silt on the exterior of the structure particles showing a tendency toward degradation and leaching as in the A_2 horizon of more typical Butler soils.

Hori- zon	Depth in.	Description
A_1	0- 6	Dark gray (10YR 4/1 dry) to black (10YR 2/1 moist) granular, friable silt loam; faint platiness in the upper one inch; pH 6.5
A_2	6- 7.5	Grayish brown (10YR 4.5/2 dry) to very dark

brown (10YR 2/2 moist) coarse granular, friable silty clay loam; contains a faint sprinkling of gray, leached silt on the structure particles; pH 6.5

B_{2-1}	7.5-18	Dark grayish brown (10YR 4/2 dry) to very dark grayish brown (10YR 2/3 moist) blocky clay; hard when dry; pH 7.0
B_{2-2}	18-22	Olive brown (2.5Y 4/4 dry) to dark grayish brown (10YR 4/2 moist) light clay; blocky; moderately hard when dry; pH 7.5
B_{2-3}	22-25	Light olive brown (2.5Y 5/4 dry) to brown (10YR 5/3 moist) blocky silty clay; moderately friable; contains an occasional small lime concretion, otherwise not calcareous; pH 7.7
B_3	25-28	Yellowish brown (10YR 5.5/4 dry) to dark yellowish brown (10YR 4.5/4 moist) silty clay or light silty clay; medium blocky; moderately friable; scattering of lime concretions; pH 7.8
C_1	28-36	Light yellowish brown (10YR 6.5/4 dry) to yellowish brown (10YR 5.5/4 moist) friable silty clay loam; ill-defined blocky structure; concretionary and disseminated lime; pH 7.8

The A_1 and A_2 horizons are moderately plastic, and the remaining horizons are very plastic and sticky when wet.

The monolith was taken in a good stand of western wheat grass only 50 feet from a trench in the big bluestem-little bluestem relict type where two others were obtained. Recent rains had wet the Butler silt loam to a depth of 5 to 6 inches, or nearly through the 7.5-inch A horizon. Exceptions occurred where water entered the large soil cracks and penetrated
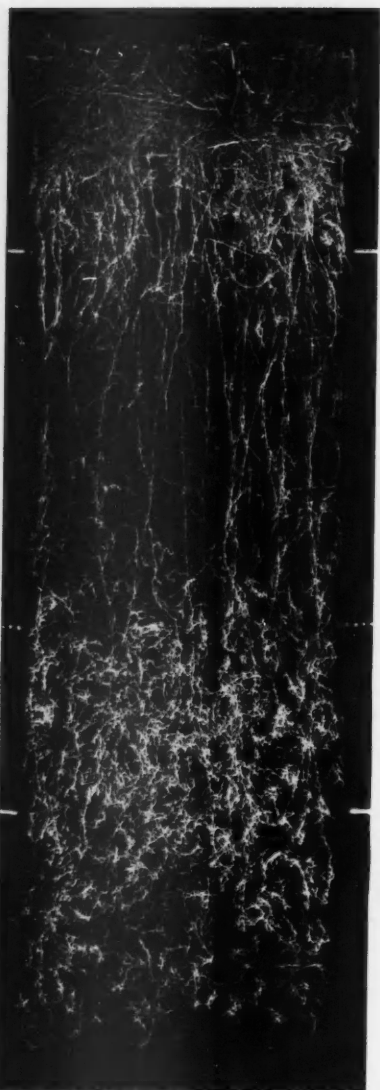
FIG. 14. Root system of western wheat grass from a 3-foot monolith of claypan soil, (6) Butler silt loam, near Carleton, Nebraska, showing the profound differences in the root habit in the three soil horizons. There are far fewer roots in the shallow A horizon (above upper lines) than is normal in mellower soils. Branching in the B horizon (above lower lines) is poor except in the lower third. But, as in the preceding sample, it is pronounced in the mellow, moist soil of the C horizon. Dots indicate a depth of 20.5 inches.

deeply, in one place to 29 inches. The entire B horizon (7.5-28 in.) was so hard that the soil was removed only with extreme difficulty. The soil was cracked to a depth of about 22 inches. These cracks below 8 in. depth, were as wide as $\frac{3}{8}$ inch. The B horizon broke out in large blocks because of the wide, nearly verti-

cal cracks. A pick was constant'y employed. The roots penetrated the B horizon with difficulty and probably (except in cracks) only when the soil was moist. They were nearly always more or less flattened and in the upper half of the horizon more poorly branched than in either the A or C horizon (Fig. 14).

At 28 inches depth, the yellowish, less compact, lime-flecked parent material of the C horizon was encountered. Here, as in the lower third of the B horizon, branching of roots was pronounced; many of the branches were short, flattened, and greatly enlarged. They penetrated the soil in all directions and produced a dense network.

The heavy branching began near the bottom third of the B horizon at 20.5 inches in depth. The weight of the roots in the 13 inches above this depth in the B horizon (7.5 to 20.5 inches) was actually less than that in the 13 inches below this level (20.5 to 33.5 inches). The increase in weight at the greater depth was 36.5 percent. There were only a few roots that penetrated beyond 36 inches.

Aside from the surface 6 inches, the root system was very much lighter than that of the preceding sample, except in the third foot where the oven-dry weights were approximately the same (Figs. 9, 13, and 14).

ROOT DEVELOPMENT IN ADJACENT SOIL

Quite in contrast was the root development of both big bluestem and little bluestem in a heavy (7) Crete silt loam soil only 50 feet distant where wheat grass had not invaded. Here the elevation was slightly less than that of the surrounding Butler soil. The A horizon was 11 inches thick and the B horizon extended to 3 feet.

7. CRETE SILT LOAM, THICK SOLUM

The several horizons and subhorizons of this soil are thicker than common for the general run of Crete soils, and no free carbonate of lime occurs in the soil to the depth sampled.[1] The texture, structure, and consistence of the various horizons are about typical of Crete soils; they are gradational from one to the other. Horizons described as friable in the dry and slightly moist state are plastic and sticky when wet.

Hori-zon	Depth in.	Description
A_{1-1}	0- 7	Very dark gray (10YR 3.5/1 dry) to black (10YR 2/1 moist) friable, fine granular heavy silt loam; pH 6.5
A_{1-2}	7-11	Dark grayish brown (10YR 4/2 dry) to very dark brown (10YR 2/2 moist) medium granular, friable silty clay loam; pH 6.5
B_1	11-16	Dark grayish brown (10YR 4/2 dry) to very dark brown (10YR 2/2 moist) fine nuciform, friable silty clay; pH 6.5
B_{2-1}	16-22	Dark brown (10YR 3/3 dry) to dark brown (10YR 3.5/3 moist) medium nuciform, moderately friable light clay; pH 6.5

[1] The sample is from an area where the parent loess is low in lime. J. C. Maker, Isomarmor. Map of the Peorian loess in Nebraska, 1935-1936 (unpublished).

B_{2-2} 22-28   Dark brown (10YR 3/3 dry) to dark brown (10YR 3/3 moist) medium nuciform, moderately friable light clay; pH 6.5

B_3 28-36   Light olive brown (2.5Y 5/4 dry) to brown (10YR 5/3 moist) medium blocky, moderately friable silty clay loam; pH 6.8

C_1 36-47   Light yellowish brown (2.5Y 6/4 dry) to yellowish brown (10YR 5/4 moist) medium blocky, moderately friable silty clay loam; some faint stainings and mottlings of brown in the interiors of the structure particles; pH 7.0

C_2 47-48   Light yellowish brown (10YR 6.5/4 dry) to light olive brown (2.5Y 5/4 moist) irregular medium blocky, friable silty clay loam; mottled with light gray and brown; pH 7.0; no free carbonate of lime

This black granular soil had been uniformly wet by recent rains to a depth of 9.5 inches. In fact, the soil was moist at all depths to 5 feet. No cracking was observed. It was a heavy type of soil, yet the roots of the grasses extended nearly to or somewhat beyond the 4-foot depth of the monoliths (Figs. 15 and 16). The roots were extremely well developed. They were consistently of greater weight in each foot of soil than those in (4) Judson soil at Lincoln, although the growth of tops was somewhat less.

It is important to note that the horizons of Crete soils are more gradational with one another than are those of the planosolic Butler soils, and that the Crete has no A_2 horizon above the heavy but well-structured B horizon.

The (6) Butler silt loam prevailed to the edge of the (7) Crete silt loam with the bluestem grasses. The relict grasses were bounded on three sides by wheat grass or wheat grass and buffalo grass growing in the Butler silt loam. On the remaining side there was cultivated land. By probing with a soil tube, the very compact B horizon was found to occur at 6.5 to 8.5 inches depth in all places surrounding the bluestem prairie. The transition from one soil type to the other was clearly indicated by the change from bluestems to wheat grass; the ecotone where these grasses were mixed was only a yard or two in width. Further examination revealed that the Butler soil formed a rim several rods wide about the patch of bluestems but farther outward gave way to Crete silt loam which was also clothed with western wheat grass. The soil under bluestems probably receives more water than the surrounding area, but the water does not stand long enough to cause a true claypan. This rim of Planosol (true claypan) about it on three sides is not an unusual phenomenon.

WESTERN WHEAT GRASS IN (8) SCOTT SILTY CLAY LOAM

There is a large area of Scott soil in a depression about a mile wide, probably an old lagoon, 2.5 miles west of Bruning, which is near Carleton, Nebraska. It is covered largely with native vegetation, much of which is western wheat grass. The wheat grass was of only moderate density and height.

8. SCOTT SILTY CLAY LOAM

This sample is a variant of the Scott soils that lacks the well-developed light gray A_2 horizon. In many
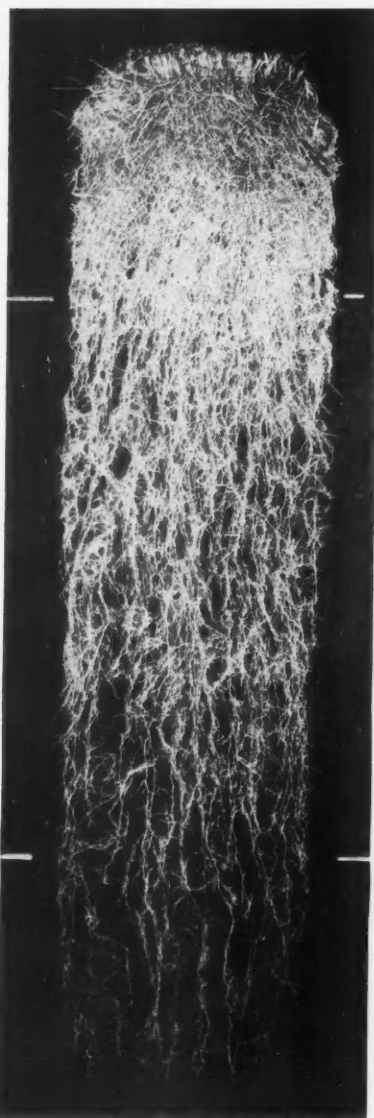
FIG. 15. A very heavy root system of little bluestem from a 4-foot monolith taken only 50 feet from that in figure 14. There is a uniform decrease of roots with depth in this (7) Crete silt loam with a thick solum, although 85 percent of the root-weight is in the A horizon. The longest roots attained a depth of 46 inches.

places free lime carbonate is leached to greater depths in Scott soils.

Hori-zon	Depth in.	Description
A_1	0- 5	Dark gray (10YR 4.5/1 dry) to very dark gray (10YR 3/1 moist) platy, friable silty clay loam; pH 6.5
B_2	5-41	Gray (10YR 5/1 dry) to dark gray (10YR 4/0) compact dense clay; very hard when dry; cracks

when dry to form large irregular columns; irregular
horizontal breakage of columns forms large irregular
blocks. The lower part of this horizon is grada-
tional in color and texture to the third (C) horizon.
A sprinkling of soft iron or manganese concretions
(1 to 5 mm. in diameter) occurs throughout this
horizon; pH 6.5

C   41-48   Light gray (10YR 7/2 dry) to light brownish gray
(10YR 6/2 moist) massive silty clay; contains a
sprinkling of lime concretion, otherwise not cal-
careous; pH 7.5

All horizons are plastic and sticky when wet.

The top soil, including 2 inches of dust deposit, is
only 5 to 6 inches thick. Below this lies the claypan
of the B horizon. It was impossible to remove this
layer until a crack was found that had let the water
from recent rains infiltrate and thus soften the soil.
The tiling spade could not be forced into the soil
except by striking the top of the blade repeatedly
with a sledge hammer. Many strokes of the hammer
were required to sink the spade even a few inches in
depth. Numerous cracks were observed in the trench
wall, some were a half-inch in width. They resulted
from the shrinking of the clay into large blocks and
columns, some of which were a foot or more thick.
The soil was so compact and heavy that it required
seven hours of very hard work by three experienced
men, who would have dug a similar trench in ordinary
soil in two hours. The roots penetrated the prisms
and blocks of soil throughout probably at a time when
they were wet or at least very moist. This is quite
in contrast to the behavior of the bluestems which in
hard soils (but not so compact as this) often leave
lumps and clods unpenetrated. Many if indeed not
most of the roots were flattened and thickened. The
branches were often short. Other roots were of normal
circular area in cross-section. The soil seemed to be
well threaded by them but no other data could be
obtained in digging except as to their presence or ab-
sence and abundance. It was difficult to crush the
lumps even with a sledge hammer.

In the dark gray, thick B horizon (5-41 in.) the
soil was much compacted. It became slightly less
difficult to remove at a depth of 35 inches. Lime con-
cretions appeared in the C horizon at a depth of 45
inches. But even here the soil was firmly compacted.
In the 4-foot monolith taken between two large cracks,
the roots did not extend below 31 inches.

After a long period of soaking and intervals of
washing, the root system was secured in its entirety
(Fig. 17). In fact, contrary to the expectations of
the authors and the soil examiners, when the soil be-
came thoroughly wet and swollen it washed away from
the roots quite readily. The primary components
were particles of small size. Root branching was
especially poor in the upper portion of the claypan.
It increased somewhat with depth. It was very pro-
nounced below 20 inches, that is, in the lower half
of the second and upper half of the third foot.

Roots in the cracks on each side of the monolith
penetrated to a maximum depth of 40 inches. "Dry
weather so shrinks and cracks many of the claypans
that water penetrates them readily following dry
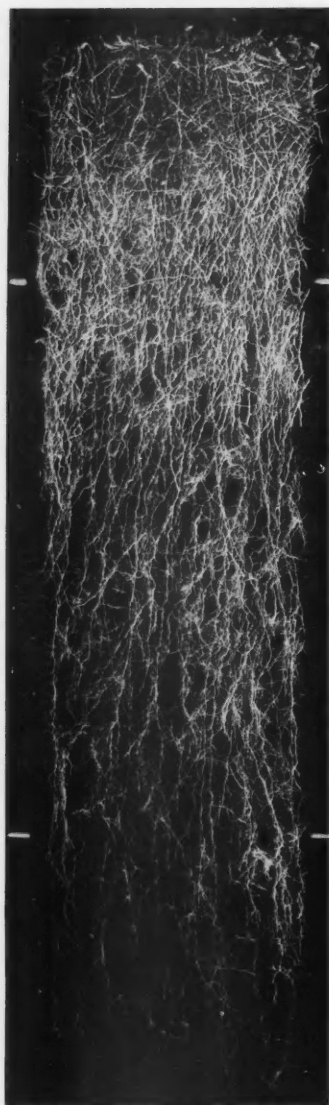
FIG. 16. Roots of big bluestem taken from the same
trench as the little bluestem. The roots are most abun-
dant in the A (0-11 in.) horizon despite the fact that
the B horizon (11-36 in.) is 25 inches thick. Total
weight of these coarser roots was about the same as those
of little bluestem (Fig. 15).

weather. Grass roots work their way between the
blocky- and prismatic-structured particles into deeper
layers of the subsoil in search of moisture, and some
of the roots actually pierce the dense blocks and
prisms of clay. Such penetration tends to lessen the
undesirable physical conditions of the soil. Shrinking
and expanding of the clay blocks with changes in
moisture have the effect of flattening the roots, but
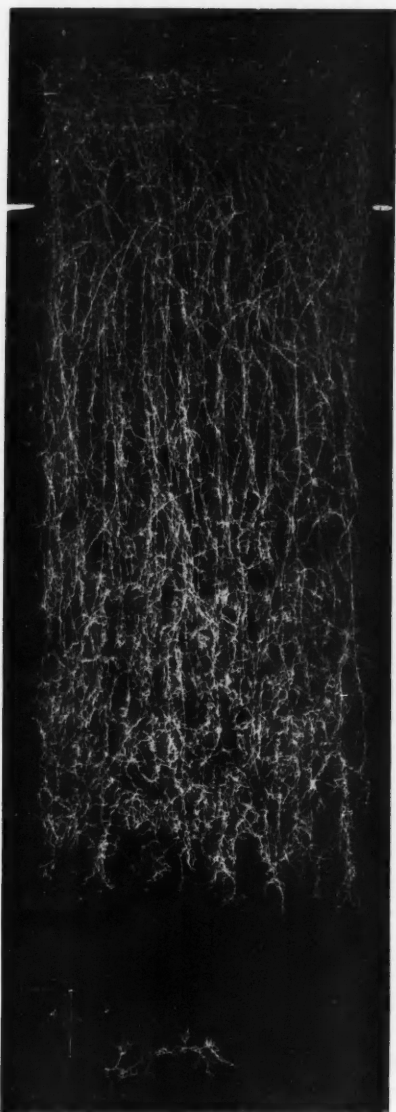
FIG. 17. Root system of western wheat grass washed from a 4-foot monolith of (8) Scott silty clay loam which had a thick claypan. Roots were not of usual abundance even in the shallow A horizon (0-5 in.). They were sparse and relatively poorly branched in the upper portion of the B horizon (i.e. 5 to 20 inches depth) but branching increased at greater depths and continued to the root-ends at 31 inches. The isolated root at 37 inches depth is a branch from a root which penetrated deeply in a large crack at the side of the monolith.

this process does not kill them except where extreme shrinkage in dry weather breaks them asunder. Only in soils with subsoil horizons very low in plant nutrients and moisture do the roots fail to penetrate the claypans" (Thorp 1948).

One root entered the monolith at 37 inches depth (Fig. 17). Like the others, it was profusely branched but mostly with relatively short laterals. As in (6) Butler silt loam, the laterals were shorter but heavier than normal. Many were not only flattened but also thickened in all dimensions. The branches ran in all directions, downward, horizontally, or even vertically upward, probably extending into the most penetrable part of the soil mass. Amount of root material was small compared with that from the wheat grass in (5) Crete silty clay loam near Lincoln.

WESTERN WHEAT GRASS IN RENDZINA SOIL

Four miles east of Belleville, Kansas, and 45 miles southeast of Carleton, western wheat grass has occupied a well drained lowland, surrounded on three sides by steep slopes, for a long period of time. Before the great drought of 1933 to 1940 this was the only place that wheat grass occurred in this bluestem prairie. It remained as a pure stand during the drought and also during seven years of postdrought, big bluestem being unable to replace it. This soil was presumed to have a claypan.

Upon digging a trench no claypan was found, but the soil had a clayey subsoil in which the blocky and nuciform aggregates were strongly developed and quite stable. Consequently the material was removed from the roots only with extreme difficulty. At 38 inches in depth this heavy soil gave way abruptly to a hard, unweathered limestone which formed a barrier to water penetration in the soil and probably caused it to be very wet and poorly aerated during periods of high rainfall. In this respect it was similar to soil with a claypan, which may explain the absence of the bluestems.

9. RENDZINA SOIL OF THE CHERNOZEM ZONE; SERIES NAME NOT DETERMINED

This soil in its morphological aspects is quite typical of Rendzinas of the Chernozem zone. It is developed in local alluvium-colluvium from the surrounding slopes over weathered limestone, plus probably a thin covering of loess. It is mildly calcareous in the upper horizon and strongly calcareous in succeeding horizons. The associated Bloomington soils are normally leached of free carbonates to a depth of one to two feet and are neutral or slightly acid in the surface and upper subsoil layers. The B_1, B_3, and C_1 horizons are plastic when wet.

Horizon	Depth in.	Description
A_{1-1}	0- 8	Very dark gray (10YR 3/1 dry) to black (10YR 2/1 moist) silty clay loam; friable; granular; mildly calcareous; pH 7.3
A_{1-2}	8-10	Dark gray (10YR 4/1 dry) to very dark grayish brown (10YR 3/2 moist) silty clay loam; coarse granular or nuciform structure; friable, calcareous; pH 7.5
B_{1-1}	10-20	Light brownish gray (2.5Y 6/2 dry) to dark grayish brown (10YR 4/2 moist) silty clay; irregular, weak, blocky; breaks easily to medium and fine nuciform particles; contains a few soft fine fragments of weathered rock; these are light brown and yellowish brown in color and crush

easily to a powdery very fine sand or silt mass; strongly calcareous; pH 7.5

B₃ 20-27 Light gray (2.5Y 7/2 dry) to light olive brown (2.5Y 3.5/4 moist) silty clay loam; medium blocky; moderately friable; weathered rock fragments are more numerous than in layer above; strongly calcareous; pH 7.5

C₁ 27-36 Light gray (10YR 7/3 dry) with yellow mottlings (2.5Y 7/6 dry) to light brownish gray (2.5Y 6/2 moist) with yellow mottlings, silty clay loam; friable; shows stratification of alluvial deposition or of weathered stratified bedrock; strata are separated by thin lenses or a sprinkling of fine sand; contains weathered rock fragments as in

the layer next above; strongly calcareous; pH 7.5

C₂ 36-38 This is like the layer next above, except that it contains shell fragments from the weathered limestone

D 38 Limestone bedrock

The general appearance of the root system, which branched profusely in the bottom of the B horizon and especially in the C horizon (27-38 in.), was similar to the preceding (Fig. 18). There was a distinct thinning of the root mass in the B horizon and a great increase in branching in the C layer. Here the roots often occurred in small bundles or groups of 5 to 13. A mat of roots 2 to 3 mm. thick was lifted from the rock in places while many roots were firmly attached to it elsewhere (Fig. 19).

Fig. 19. Roots of western wheat grass matted on the rock (left), and root-mats lying just above it (right). These were taken at a depth of 38 inches in a Rendzina soil.

ROOT DISTRIBUTION IN MELLOW LOESS SOILS

In central Nebraska there are several thousand square miles of loess hills. Much of this area is range land and is clothed with short grasses, the roots penetrating deeply or more shallowly depending upon the texture, structure, maturity, and stability of the various types of soil. In general the soils are very fine textured, consisting mostly of silt, approximately a third of clay, and smaller percentages of very fine sand. The organic matter usually ranges from 4 to 4.5 percent and the total nitrogen often ranges from 0.13 to 0.20 percent. The soil is highly erosive. Precipitation at Kearney, where these studies were made, is 23.9 inches.

BLUE GRAMA IN (10) HASTINGS SILT LOAM

Roots from the monolith taken on a nearly level hilltop in the Sheen pasture are shown in figure 20. There was a good stand of blue grama in the deep silt loam soil which is a fairly representative sample of Hastings silt loam, a typical Chernozem. It is interesting to note that here there is a typical Chernozem on the smooth hilltop associated closely with the Sherman silt loam, a Chestnut soil on the adjacent
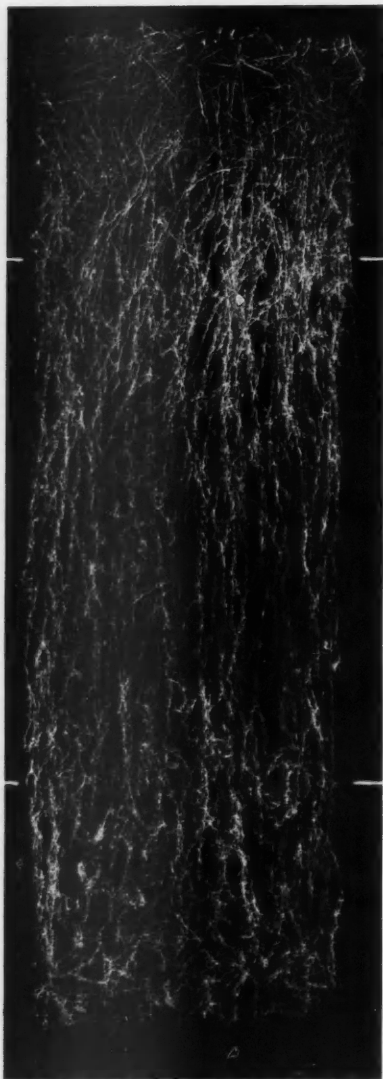

Fig. 18. Three feet of roots of western wheat grass from a monolith of Rendzina soil underlain by unweathered limestone in a ravine. There is no increase in root-weight in the third foot over that of the second, but a great increase in branching.
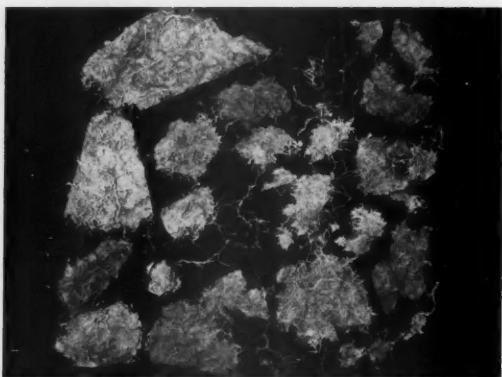
FIG. 20. Upper 4 feet of the root system of blue grama in (10) Hastings silt loam on a loess hill near Kearney. Note the great density of the root mass in the A horizon (0-15 in.). This, when dried, was found to compose 91 percent of the entire root-weight; only about 8 percent was found in the B (15 to 35 in.) horizon. But some absorption also occurred in the C horizon.

rather steep slope. At least part of the differences between the two soils can be ascribed to differences in moisture relationships brought about by differences in slope gradient. Also important is that the Hastings silt loam shows little or no evidence of a second soil formed from relatively new loess in the upper part of the profile as does the Sherman silt loam to be described.

10. HASTINGS SILT LOAM

Hori-zon	Depth in.	Description
A_1	0- 8	Dark gray (10YR 4/1 dry) to black (10YR 2/1 moist) silt loam; soil breaks into thin plates and fine granules; friable; pH 7.0
A_3	8-15	Very dark grayish brown (10YR 3/1.5 dry) to very dark brown (10YR 2/2 moist) heavy silt loam; granular structure; friable; pH 7.0
B_2	15-25	Dark grayish brown (2.5Y 4.5/2 dry) to very dark grayish brown (2.5Y 3.5/2 moist) heavy clay loam; fine prismatic aggregates breaking into blocks; plastic; pH 7.3
B_3	25-35	Light olive brown (2.5Y 5.5/4 dry) to olive brown (2.5Y 4.5/4 moist) light silty clay loam; blocky structure; moderately friable; pH 7.5
C_1	35-48	Light yellowish brown (2.5Y 6.5/4 dry, with white spots) to light olive brown (2.5Y 5.5/4 moist, with white spots) heavy silt loam; massive; friable; calcareous

Roots were especially abundant in the deep A horizon (0-15 in.). At greater depths roots were fewer but they continued to branch profusely to a depth of 4 feet. A few extended beyond the monolith to approximately 5 feet.

BLUE GRAMA IN (11) COLBY SILT LOAM

Quite in contrast to this excellent development was the much lighter root system obtained from Colby silt loam under approximately the same mean annual rainfall of about 23 inches. The monolith was taken on a slope of only 3 percent gradient in a large prairie 5 miles southeast of Broken Bow, Nebraska.

11. COLBY SILT LOAM [1]

The so-called Colby silt loam is typical of the soil as mapped in much of central and western Nebraska, but is leached somewhat deeper and has a slightly thicker dark surface soil than some Colby soils in this state. Much of the Colby soil of Nebraska is essentially the same in texture throughout the profile.

Hori-zon	Depth in.	Description
A_{1-1}	0-3/4	Grayish brown (10YR 4/2 dry) to dark grayish brown (10YR 3/2 moist) silt loam; medium to fine crumb structure; friable; pH 7.0
A_{1-2}	3/4- 4	Grayish brown (10YR 5/2 dry) to grayish brown (10YR 4/2 moist) silt loam; granular or crumb structure; friable; pH 7.0
A_{1-3}	4-12	Grayish brown (10YR 4.5/2 dry) to dark grayish brown (10YR 3.5/2 moist) heavy silt loam; granular structure with prismatic cleavage; friable when moist, slightly plastic when wet; pH 7.0
B_1	12-20	Grayish brown (10YR 5/2 dry) to grayish brown (10YR 4/2 moist) light silty clay loam; medium prismatic and nuciform granular structure; slightly plastic when moist to plastic when wet; pH 7.0
C_1	20-32	Olive brown (2.5Y 5.5/3 dry) to dark olive brown (2.5Y 4.5/3 moist) silt loam; prismatic and coarse nuciform structure; friable; pH 7.5
C_2	32-46	Light olive brown (2.5Y 6/3 dry) mottled with yellowish brown (10YR 5/4 dry) to grayish

[1] This soil has been called Colby silt loam over a wide area in Nebraska, but it is darker colored than the Colby silt loam of eastern Colorado and western Kansas. It resembles closely the Ulysses silt loam, a series recognized tentatively in western Kansas.

brown (2.5Y 4.5/2 moist) mottled with yellow-
ish brown (10YR 4/4 moist) silt loam; coarse
prismatic structure; friable; calcareous; pH 8.0

C₃　46-48　Light brownish gray (2.5Y 6/2 dry) mottled
white (2.5Y 9/2 dry) to grayish brown (2.5Y
4.5/2 moist) mottled white (2.5Y 8/2 moist)
silt loam; coarse prismatic structure grading to
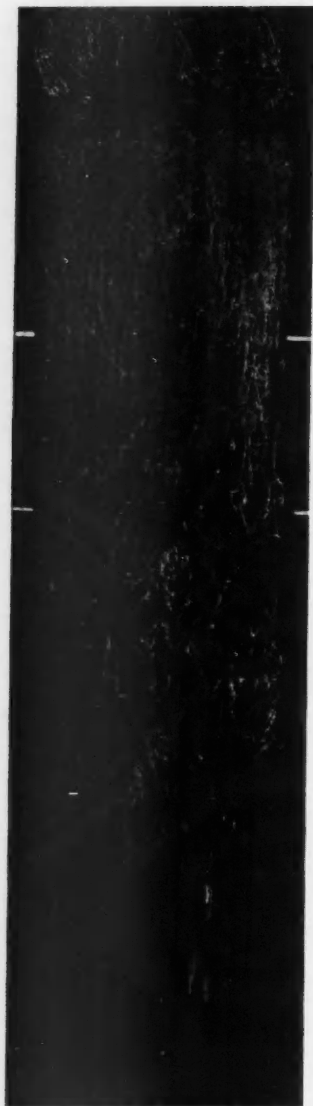massive; very friable; calcareous; pH 8.0 +

FIG. 21. Four feet of the root system of blue grama
in (11) Colby silt loam. There is much less root material
at all depths than in the same species growing in the
more mature (10) Hastings silt loam, in figure 20.

Even casual examination of figure 21 shows that
greatest concentration of roots was in the A horizon
(0-12 in.) of this shallow solum. Even this layer was
relatively poorly occupied; one-fourth less material

was found here than in the first foot in the heavier
(10) Hastings silt loam. Differences at greater depth
were even more marked. Depth of penetration was
approximately 5.5 feet, the roots ending in very moist,
limy parent loess.

BUFFALO GRASS IN (12) HOLDREGE SILT LOAM

The roots in a uniformly thick, pure stand of *Buch-
loe dactyloides* were studied on a nearly level upland
in the McCan experimental pasture 1 mile northwest
of Kearney, Nebraska (Weaver & Bruner 1948). The
soil is Holdrege silt loam. It has about the maximum
content of clay in the B horizon for this type but it
is definitely within the range of the Holdrege series.

12. HOLDREDGE SILT LOAM

Hori-zon	Depth in.	Description
Recent dust accumulation	0- 1	Grayish brown (10YR 5/2 dry) to very dark grayish brown (10YR 3/2 moist) silt loam of fine-crumb structure; friable, dry and moist; pH 6.5
A₁₋₁	1- 6	Dark grayish brown (10YR 4/1.5 dry) to very dark grayish brown (10YR 3/1.5 moist) silt loam; fine-crumb structure, vertical cleavage; friable, dry and moist; pH 6.5
A₁₋₂	6-12	Dark grayish brown (10YR 4/2 dry) to very dark grayish brown (10YR 3/2 moist) silt loam; strong, fine to medium granular structure, vertical cleavage; friable, dry and moist; pH 6.8
B₁	12-15	Dark grayish brown (10YR 4/2 dry) to very dark grayish brown (10YR 3/2 moist) light silty clay loam; prismatic-nuciform-granular (compound) structure with strong vertical cleavage; friable, dry; slightly plastic, moist to wet; pH 6.8
B₂₋₁	15-22	Grayish brown (10YR 5/2 dry) to dark grayish brown (10YR 4/2 moist) silty clay loam; prismatic-nuciform-granular (compound) structure with strong vertical cleavage, primary aggregates 1/2 to 3/4 inch in diameter; friable, dry; moderately plastic, moist and wet; pH 7.0
B₂₋₂	22-28	Light brownish gray (10YR 6/1.5 dry) to grayish brown (10YR 5/1.5 moist) silty clay loam; imperfect prismatic-nuciform structure; friable, dry; moderately plastic, moist and wet; pH 7.0
B₃	28-36	Light yellowish brown (2.5Y 6/3 dry) to light olive brown (2.5Y 5/3 moist) heavy silt loam; imperfect prismatic, weakly nuciform secondary aggregates; friable, dry; slightly plastic, moist and wet; pH 7.5
Bca or C₁	36-48	Mottled pale yellow and white (2.5Y 7/4, 8/1 dry) to light yellowish brown (2.5Y 6/3 moist) silt loam; prismatic to massive structure; friable, moist and dry; pH 8.0; soft lime carbonate; lime concretions

The roots were traced in the walls of a trench to
a depth of 6 feet, where they ended after extending
well into the lime layer. But in one end of the trench
deep soil was dry and no roots were found beyond
4.5 feet. Those obtained in a monolith 4 feet long
are shown in figure 22. Although these fine, tough
roots were branched throughout their length, the
greatest branching occurred in the A horizon (0-12
in.) and its transition into the B horizon (B₁ 12-15
in.). At greater depths they decreased very rapidly
in dry weight. The uniformity of distribution is in-
teresting and the depth remarkable for a low-growing
grass that was frequently moderately grazed to a
height of 2.5 inches.

FIG. 22. Root system of buffalo grass *(Buchloe dacty-loides)* taken from Holdrege silt loam on a nearly level upland near Kearney, Nebraska. The roots are from a 4-foot monolith. There were about 330 main roots at a depth of 6 inches but only 153 at 12 inches depth. At 2, 3, and 4 feet the numbers were 51, 30, and 22, respectively.

This well developed root system appears very similar to that of blue grama with which this species is often associated in the same type of soil. It differs, however, in two respects. Underground parts in the 0-6 inch layer were 49 percent greater in blue grama in (10) Hastings silt loam. But below 3 feet materials were only half as great as in buffalo grass in (12) Holdrege silt loam.

BUFFALO GRASS IN (13) WABASH SILT LOAM

The flat-bottomed valleys between the hills were originally clothed with bluestems, perhaps chiefly big bluestem. During a long period of settlement and grazing by livestock the original vegetation had been replaced by a stand of buffalo grass. This had effectually prevented erosion, at least in the upper part of the valley. The buffalo grass flourished even under constantly close grazing (usually to about 1.5 inches) from early spring until late fall (Weaver & Bruner 1948). During these years a fill of 12 inches from silty upland soils had been washed in on top of the former soil.

The monolith was taken from bottomland in the McCan pasture, 1 mile northwest of Kearney. The exact correlation of this soil is not presently known, but it has many characteristics like the Wabash silt loam, developed from recent alluvium, farther east in Nebraska. For practical purposes, it could be grouped with the Wabash silt loam, even though a careful field study may show that another name would be better. The Wabash silt loam has commonly been classified as an alluvial soil, which means that it is essentially stratified alluvial deposit in which there has been very little soil development. Actually most of the Wabash soils have been in place long enough for much organic matter to accumulate. Furthermore, drainage in Wabash soils is imperfect, and the relatively high water table causes a rather strong mottling and streaking in the lower part of the profile. This would tend to place the soil in the category of Wiesenboden (imperfectly drained meadow) soils. Wabash soils are associated most typically with the black Prairie soils of Iowa and eastern Nebraska. This soil is associated with the Chernozems of central Nebraska.

13. WABASH SILT LOAM IN CHERNOZEM AREA

Horizon	Depth in.	Description
(Fill)	0-12	Grayish brown (10YR 5/2 dry) to very dark grayish brown (10YR 3/2 moist) light silty clay loam; laminated; friable; pH 7.0
A_{1-1}	12-26	Dark gray (10YR 4/1 dry) to black (10YR 2/1 moist) heavy silt loam; medium granular structure; friable; pH 7.0
A_{1-2}	26-36	Grayish brown (2.5Y 5/1.5 dry) to very dark grayish brown (2.5Y 3/1.5 moist) light silty clay loam; granular to weakly prismatic; friable; pH 6.5
C_1	36-44	Light yellowish brown (2.5Y 6/3 dry), streaked with brown and light gray, to light olive brown (2.5Y 5/3 moist), also streaked, light silty clay loam; weakly granular structure; friable; pH 6.0
C_2	44-48	Light olive brown (2.5Y 5/3 dry), streaked with brown and light gray, to slightly darker colored moist; silt loam; laminated; friable; pH 6.0

When the roots were examined in a deep excavation they were found in abundance to 5 feet in depth and some extended to 6.5 feet. Those from a 4-foot monolith are shown in figure 23.

The mass of roots was especially dense in the 12 inches of fill. But even to a depth of 2.5 feet the root system was remarkably developed. The deep, well drained soil was usually more moist and also wet
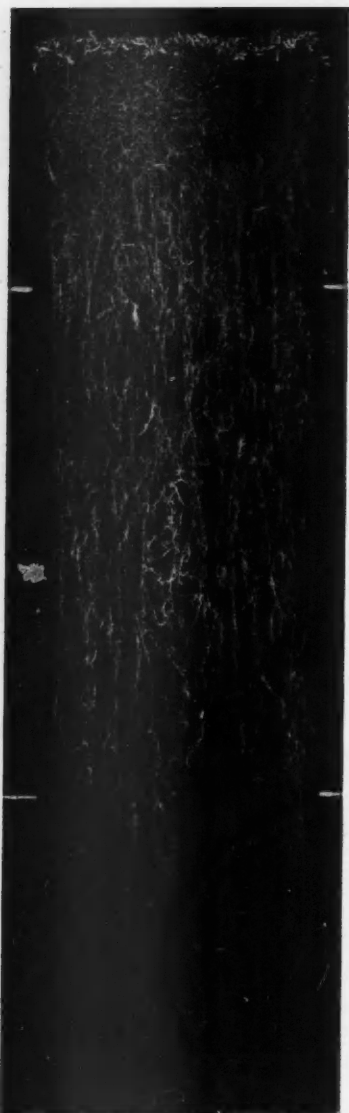
FIG. 23. Four feet of roots of buffalo grass taken from Wabash silt loam in a valley about 300 yards from the trench in Holdrege silt loam on the hilltop. Note how much deeper than in figure 22 the massive portion of the root system extends. Upper lines mark the depth of the 12-inch fill; lower ones the depth of the A horizon, 36 inches.

to a greater depth than that of the upland from which snow was blown and runoff water ran down the slopes. Moreover, these loess soils are fairly low in both nitrogen and phosphorus. Undoubtedly supplies of these nutrients were greater in the lowland soils as a result of the soil and organic matter deposited there. Organic phosphorus is most readily available to the growing plant, and this too may have promoted greater

root development, despite the more constant and closer grazing, than on upland. A comparison of figure 23 with figure 22 clearly reveals a much heavier root system in the (13) Wabash silt loam. Dry weight of underground parts in grams in the first two 6-inch levels and then foot by foot was consistently less in (12) Holdrege silt loam. They were as follows: 15.1 and 17.1; 2.5 and 2.9; 2.4 and 2.6; 0.8 and 1.3; 0.6 and 0.7.

BUFFALO GRASS IN (14) SHERMAN SILT LOAM

This monolith was taken from a slope in Sheen's pasture 4.5 miles west and 1 mile north of Kearney (Weaver & Bruner 1948). There was an excellent stand of buffalo grass. The slope had a gradient of 11 percent with a westerly aspect. While this soil occurs in the Chernozem zone, it is near the zone's western edge, and the soil itself has more characteristics like Chestnut soils than like Chernozem soils. Probably this is because the rather steep gradient of the land and the slope toward the west had reduced the effectiveness of the moisture. It appears that the soil as sampled actually has a "double profile." The soil at a depth of 17 inches represents the original surface on which a rather well-developed Chernozem soil was formed. Following the formation of this Chernozem soil, loess was deposited to a depth of about 17 inches and a new soil was formed from this new loess deposit. Hence, there is a succession of A_{1-1}, A_{1-2}, and A_3 horizons underlain by the old A_{1-1} and A_{1-2} horizons that were formed before the material of the upper part of the soil was deposited. This explains the peculiar designations of horizons which appear in the following description. The closest correlative of this soil is the Sherman silt loam, and it is believed that this correlation will be satisfactory.

14. SHERMAN SILT LOAM

Horizon	Depth in.	Description
A_{1-1}	0- 6	Dark grayish brown (10YR 4/1.5 dry) to very dark grayish brown (10YR 3/1.5 moist) heavy silt loam that breaks easily into granules averaging about 2 mm. in diameter; friable; pH 6.8
A_{1-2}	6-11.5	Brown (10YR 5/2.5 dry) to dark brown (10YR 4/2.5 moist) heavy silt loam; granules 2 mm. in diameter; friable; pH 7.0
A_3 (transition)	11.5-17	Brown (10YR 5/2.5 dry) to dark brown (10YR 4/2.5 moist) heavy silt loam that breaks first into small prisms and then into medium-sized granules; friable; pH 7.0
A_{1-1} (old soil)	17-23	Dark grayish brown (10YR 4.5/1.5 dry) to very dark grayish brown (10YR 3.5/1.5 moist) light silty clay loam; breaks into medium-sized prisms with weakly granular subaggregates; friable; pH 7.5
A_{1-2} (old soil)	23-29	Dark grayish brown (2.5Y 4/2 dry) to very dark grayish brown (2.5Y 3/2 moist) light silty clay loam; structure as above; friable; weakly calcareous.
B_1 (old soil)	29-36	Grayish brown (2.5Y 5/2 dry, with white spots) to dark grayish brown (2.5Y 4/2, with white spots, moist) light silty clay loam with well developed prismatic structure; friable; strongly calcareous.

This root system was somewhat better developed at all depths than either of the preceding samples of buffalo grass. In both (12) Holdrege and (13) Wabash silt loam the weight of roots in the second foot was slightly less than that in the second 6-inch layer. But in (14) Sherman silt loam there was a small increase in weight in the second foot. The A_{1-1} horizon of the old soil (17-23 inches depth) is included in the second foot and probably accounts for this increase. Three other samples of roots of buffalo grass in this soil gave similar results. Roots extended far beyond the 3-foot monolith, some reaching a depth of 6 feet.

VARIOUS SPECIES IN AZONAL SOIL OF THE LOESS

In the loess hills of central Nebraska some low-grade grasslands have resulted from abandoning cultivated land. This land was usually on such steep slopes that it should never have been broken. For many years annual and perennial weeds constitute the bulk of the scanty cover of vegetation. Perennial grasses enter and increase slowly. A part of the pasture (80 acres) from which the following monoliths were taken had been broken for raising crops and then abandoned 25 years ago. As a result erosion by wind and water had removed all of the solum (A and B horizons) over considerable areas of the steeper slopes. They were now partly clothed with small patches of blue grama, buffalo grass, and western wheat grass alternating with more extensive stands of three-awn grasses (*Aristida purpurea* and *A. oligantha*), although weeds and certain other species of grasses were common.

Monoliths were taken on a slope of 11 percent in an area mapped as Colby silt loam. There was a very thin, poorly developed new A_1 horizon only 2 to 3 inches deep. The soil is of loessal parent material, rich in lime throughout which is often in concretions, and with a pH of 8. The same light yellow color prevailed from the soil surface to 4 feet in depth. The lime layer began at a depth of 5.5 to 7.5 inches and was still present at 4 feet.

BLUE GRAMA

The soil around bunches and small patches of blue grama was often eroded several inches below the plant crowns. Sometimes living bunches of this grass extended 7 to 8 inches above the level of the surrounding soil. Although a good stand of blue grama was selected for the monolith, similar blocks of adjoining sod broke up easily as did those of all the other grasses examined. Only a very few roots extended beyond the 3-foot monolith although the soil in each of 5 trenches (except under western wheat grass) was moist to greater depths (Fig. 24). Although the weight of the upper 6 inches of roots of blue grama (28.7 gm.) exceeded that of the same species in upland Hastings silt loam (22.5 gm.), the remainder of the root system to 3 feet weighed 37 percent less. Moreover, it was 12 to 18 inches shallower.
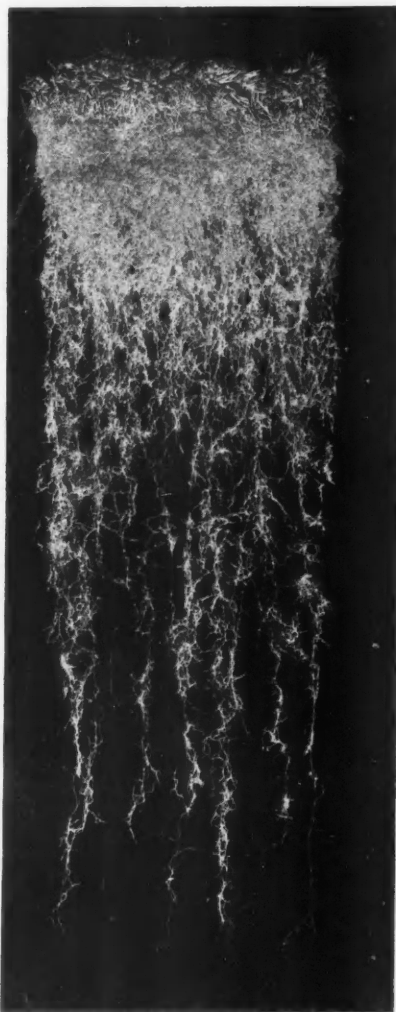
FIG. 24. Roots of blue grama in a 3-foot monolith taken in deeply eroded loess. Nearly all of the roots are concentrated in the surface 12 to 14 inches of soil. The deeper roots appear very different from those taken in mature soil (10, Hastings silt loam) in the same pasture (Fig. 20).

BUFFALO GRASS

In the patches of buffalo grass the ungrazed midsummer foliage had a height of only 1.5 to 2.5 inches. The stand was only half that on mature soil. Despite the yellow-green color and stunted condition of the foliage the plants had produced flowers and some seed. A mass of roots occurred only in the first foot. They were very thin and poorly developed deeper (Fig. 25). In the surface 6 inches the underground parts weighed only about a fourth as much as those of blue grama. At greater depths the roots were

below which they became much sparser. There were few below 2 feet and only rarely was one found deeper than the 3-foot level. Normally this species has a well developed root system 4 to 5 feet deep.

WESTERN WHEAT GRASS

Western wheat grass was taken in a monolith only a few yards distant from the preceding trenches and on the same slope. This profusely and deeply rooted species had previously been studied in the Colby silt loam in another site about half a mile distant

FIG. 25. Root system of buffalo grass to a depth of 3 feet showing the relatively poor development when growing on loess subsoil.

heavier than those of blue grama and they extended a little deeper. But only rarely was a root found below 36 inches.

Comparison was made of this abbreviated root system with that of buffalo grass growing in well developed soil (Fig. 22). The mass of buffalo grass roots in the surface 6 inches was about half that of the same grass in Holdrege silt loam. The total root weight to 3 feet in depth was only slightly more than half as great.

SAND DROPSEED

Sporobolus cryptandrus grew here in stands about two-thirds as dense as those found on mature soil. The tops were greatly dwarfed. Here also the roots in the monolith were very abundant to 15 inches depth,

FIG. 26. Roots of western wheat grass from a 4-foot monolith of azonal soil of the loess. Comparison with roots of this species in figure 9 reveals the poor development at all levels in this impoverished, immature soil.

(Weaver & Bruner 1948). There the abundant roots penetrated vertically downward, some extending into the moist subsoil to a depth of 10 feet. But on this eroded hillside the stand was only half normal and the plants were dwarfed. The roots were proportionately few. All but 4 or 5 of the deepest were taken in their entirety in the 4-foot monolith (Fig. 26). Depth of penetration seemed not to be hindered by lack of available water, since the soil was moist below 4 feet in all the trenches.

PURPLE THREE-AWN

A monolith with *Aristida purpurea* was taken on the same slope. This perennial is extremely common in subseres. As shown in figure 27, the bulk of the roots spread laterally and soon extended beyond the width of the monolith. But some grew downward in a manner similar to that of grasses previously described.
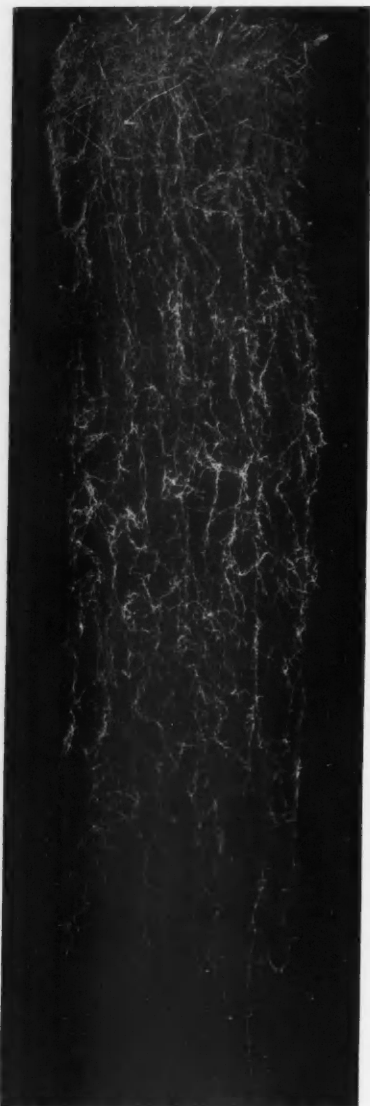
The root habits of this species have been examined by the senior author in several sites on the Great Plains of Colorado. In nearly all it was not unlike that of other grasses in regard to a rather vertical direction of penetration. The depth varied from 2.3 to 3.5 feet. Even in the exceedingly compact Pierre clay at Ardmore, South Dakota, the depth of penetration of most roots was 2.6 feet below the crown of the plant, although some penetrated 6 inches deeper. But at Yuma, Colorado, the plants grew in coarse sand which was firmly compacted. Here the roots all spread widely, even 3 to 4 feet from the crown and practically the entire root system was in the surface 2 feet of soil. In a broad valley, about a mile distant, the compacted sand was somewhat intermixed, at least near the surface, with some black soil and humus. Here the roots had a very wide lateral spread in the shallow soil. Some ran off nearly parallel with the soil surface at depths of only 2 to 6 inches for distances of about 2 feet. The surface 1.5 feet of soil was especially occupied by the coarse but well branched roots. However, about a fourth of the whole root system penetrated rather vertically downward, so that the soil beneath the plant was also well occupied (Weaver 1920). This variation of the root system of purple three-awn with the environment may be a large factor in its success in development on eroded soils.

AMOUNT OF ROOTS IN EACH FOOT OF SOIL

The actual weight and percentage of the weight of each root system that occurred in each 6 inches or foot of soil are shown in the following tables. For convenience of comparison, each species is discussed separately.

BIG BLUESTEM

There is a wide range in the weight of underground materials where big bluestem grew in different types of soil. In the surface 6 inches this range is from 16.84 to 53.49 grams (Table 2). In the second 6 inches, where the amounts are invariably much smaller, the range is from 2.02 to 8.20 grams. Without exception, roots in the second foot weighed less than those in the second 6-inch layer. Here the range

in weight is from 1.79 to 7.40 grams. Root-weight in the third foot always shows a sharp decrease over that in the second foot. The weight ranges from 0.56 to 3.70 grams. As little root-weight as 0.17 gram occurs in the fourth foot and no plant produced more than 1.24 grams. In several soil types there were no roots in the fifth foot; the largest amount recorded was 0.51 gram.

By comparing root-weight in upland soil types (2, 5, 15) it may be seen that the smallest amounts at all depths were in compacted (2) Carrington silty
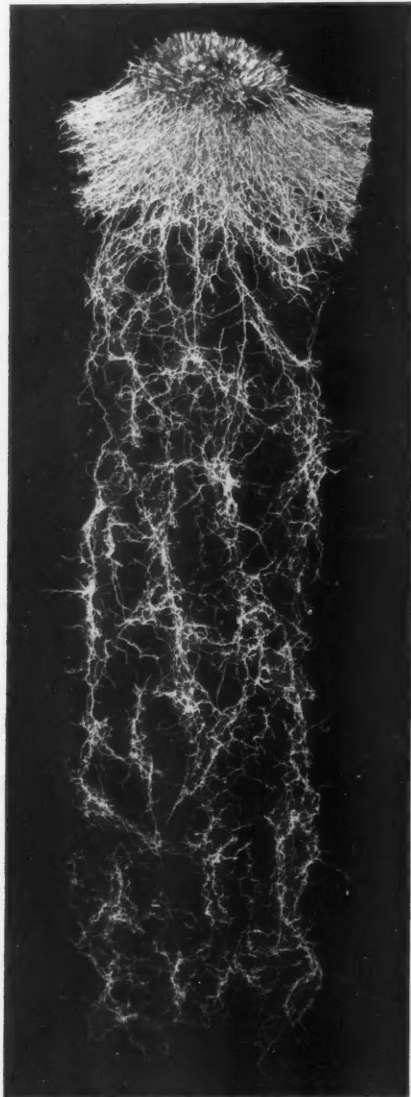

FIG. 27. Portion of the root system of purple three-awn *(Aristida purpurea)* from a 3-foot monolith taken in azonal soil. Unlike all of the preceding grasses, most of the roots spread widely in the surface soil.

TABLE 2. Distribution of root systems at each of the several depths and percentage of roots at each depth.

Spp.	Depth	2 Carrington silty clay loam		5 Crete silty clay loam		1 Sharpsburg silty clay loam		3 Wabash silty clay loam		4 Judson silt loam		7 Crete silt loam	
		gm.	%	gm.	%	gm.	%	gm.	%	gm.	%	gm.	%
A fu[1]	0- 6	17.45	75.3	28.70	78.3	33.35	77.5	16.84	78.7	33.69	68.5	35.78	63.5
	6-12	2.65	11.4	3.72	10.1	4.49	10.4	2.02	9.4	6.84	13.9	8.20	14.6
	12-24	2.34	10.1	2.60	7.1	2.95	6.9	1.79	8.4	5.15	10.5	7.40	13.1
	24-36	.57	2.5	1.19	3.2	1.35	3.1	.56	2.6	2.17	4.4	3.70	6.6
	36-48	.17	.7	.46*	1.3	.66	1.5	.19	.9	.85	1.7	1.24*	2.2
	48-60					.27*	.6			.51*	1.0		
	Total	23.18		36.67		43.07		21.40		49.21		56.32	
A sc	0- 6	P vi		37.20	65.1	44.60	85.8	A fu		53.49	80.2	45.06	75.9
	6-12	1 Sharps-		6.68	11.7	2.74	5.3	15 Crete		5.63	8.4	5.96	10.0
	12-24	burg silty		7.10	12.4	2.59	5.0	silty clay		4.19	6.3	5.26	8.9
	24-36	clay loam		2.86	5.0	1.20	2.3	loam		1.82	2.7	2.50	4.2
	36-48	Wt. of upper		2.14	3.7	.75	1.4			1.22	1.8	.62	1.0
	48-60	5 feet only		1.20**	2.1	.12	.2			.40*	.6		
	Total			57.18		52.00				66.75		59.40	
B cu	0- 6	In		24.10	85.1					33.17	85.0		
	6-12	16 Carrington		2.50	8.8					3.04	7.8		
	12-24	silty clay loam;		1.19	4.2					2.27	5.8		
	24-36	rolling phase		.55*	1.9					.56*	1.4		
	Total			28.34						39.04			
P pr	0- 6	6.78	76.3					6.59	78.1	22.04	79.9		
	6-12	1.70	19.1					1.08	12.8	2.95	10.7		
	12-24	.41	4.6					.71	8.4	2.24	8.1		
	24-36							.06	.7	.32	1.1		
	36-48									.11	.4		
	Total	8.89						8.44		27.66			

[1]A fu is *Andropogon furcatus*, A sc *Andropogon scoparius*, P vi *Panicum virgatum*, B cu *Bouteloua curtipendula*, and P pr *Poa pratensis*.
*In this table and those following, an asterisk indicates that a part of the root system, a small fraction of a gram, extended deeper than the level indicated. A double asterisk indicates that the species is deeply rooted and that much of the root system extended beyond the depth at which the monolith was taken.

clay loam. A somewhat heavier root system developed in (5) Crete silty clay loam. The monolith was from a trench only 12 feet from (5) Crete silty clay loam in which western wheat grass was taken. Wheat grass grew at one end of the trench, big bluestem at the other. The soil under wheat grass was very dry at all depths, that under big bluestem was moist. There was no soil shrinking to form cracks under the big bluestem, partly because the soil apparently had less clay. Depth and thickness of the several horizons were identical. This root development is considered by the senior author, who has examined many root systems of this grass, as approximately "normal" for upland (Fig. 28).

A far greater development of underground parts occurred in (15) Crete silty clay loam about 15 miles distant. Like the preceding it was located on a southeast slope. This slope of the 120-acre prairie had been covered with dust to a depth varying from 1 to 12 inches. The sample taken was a relict bunch of big bluestem. At this time and place the dust deposit was 3.5 inches deep. The profile was examined and the roots were separated from the soil but the description is incomplete. The depths of the A and B

horizons were 0-12 and 12-27 inches, respectively. The monolith ended in the C horizon at a depth of 60 inches. A few roots extended deeper. The soil of the B horizon was almost as heavy as that of (5) Crete silt loam from which western wheat grass was excavated.

Weight of roots in the surface 6 inches of (15) Crete silty clay loam was nearly twice as great as that of the preceding (5) and more than three times as great as that of the (2) first. Differences somewhat less pronounced also occurred in the second 6-inch layer. At greater depths the roots in this soil were heavier and they also extended about a foot deeper. This area had been covered with dust at two or more intervals during the great drought of 1934-40. As a result of this burial the rhizomes became especially heavy and woody. Normally they grow in the surface 1 to 1.5 inches of soil. Here many were 3 and some 5 inches deep. This unusual growth as a result of dust-burial has been repeatedly observed in this species. The vigorous growth of the rhizomes was reflected, it seems, in the unusual development of roots. They were much larger in diameter than those of the plants just described and were quite as large

other soil (Table 2). Roots in the second 6 inches were only half to a third or even a fourth as heavy as in the other soils. Likewise there was much less material at greater depths. This occurred despite the fact that the tops appeared to be equally well developed in all sites. Root systems in (1) Sharpsburg silty clay loam and (4) Judson silt loam were much more equally developed (Figs. 29 and 8). Those in the latter soil with the deeper A horizon and deeper solum were heavier throughout. Decrease in weight with depth was similar in these two soils. Root-weight in the surface soil was slightly greater in (7) Crete silt loam at Carleton than in the two

Fig. 28. Root system of big bluestem in (5) Crete silty clay loam without a claypan at Lincoln. The tops were well developed and the weight and distribution of roots is very usual for this species on upland. Note the greatest density of the mass of roots in the A horizon (0-12 in.). The B horizon (12-28 in.) also has a large amount of roots; only a few extended beyond the depth (48 in.) of the monolith.

as those of the best big bluestem grown on lowland. The total root-weight was 66.7 grams, compared with 36.6 grams at the other station in (5) Crete silty clay loam and 23.1 grams in (2) Carrington silty clay loam.

Of the soil types on lowland, the total underground materials in (3) Wabash silty clay loam was only half and often much less than half of that in any

Fig. 29. Root system of big bluestem from a 5-foot monolith of (1) Sharpsburg silty clay loam in a ravine at Lincoln. A few root-ends extended even deeper.

preceding soils (1 and 4) at Lincoln, despite the fact that the annual precipitation is an inch less. In this heavy type of silt loam, at the several depths from 6 to 48 inches the roots were 20, 44, 71, and 46 per-cent heavier than in (4) Judson soil near Lincoln. Total root-weight in upland soils, excepting (15) Crete silty clay loam, averaged only 29.9 grams. Root-weight in lowland types averaged 42.5 grams, or 42 percent greater.

The percentage of underground materials in the

FIG. 30. Monolith of (16) Carrington silty clay loam with the soil partly washed away. Note the concentra-tion of the roots of side-oats grama *(Bouteloua curtipen-dula)* (94 percent by weight) in the 12-inch A horizon. Only a few extended deeply.

surface 6 inches was somewhat higher in soil types on the upland (2, 5, 15) where it varied from 75.3 to 80.2. Variation in amount was greater in soil types examined in lowland (1, 3, 4, 7) where 63.5 to 78.7 percent of the underground parts were in the surface 6 inches. Percentage of root-weight in the second 6 inches varied in lowland types from 9.4 to 14.6, and in the second foot from 6.9 to 13.1. It was lower in upland soil types—8.4 to 11.4 and 6.3 to 10.1 percent, respectively.

LITTLE BLUESTEM

The greater root development of little bluestem occurred in (7) Crete silt loam at Carleton (Table 2). Although the weight of the upper 6 inches was almost identical with that in (1) Sharpsburg silty clay loam near Lincoln, there were 118, 103, and 108 percent more roots at 6-12, 12-24, and 24-36 inches depth, respectively. Hence the percentage of root distribu-tion at the various depths was also strikingly differ-ent. Total root-weights were 52.0 and 59.4 grams.

SWITCHGRASS

Switchgrass has very coarse roots which may pene-trate to depths of 9 to 11 feet (Fig. 1). The roots are much heavier than those of big bluestem from the same trench in (1) Sharpsburg silty clay loam. More-over, the weight decreases much less rapidly. Roots in the second foot (unlike those of the bluestem) exceeded in amount those in the second 6 inches. Root-weight decreased much less rapidly than in big blue-stem in the third and fourth foot. The percentages for this species are not of the entire root system but only of that part above 5 feet. The number of the coarse fibrous roots in the monolith decreased with depth as follows: at 6 inches there were 89; at 12 inches, 77; then by foot depths, 46, 21, 16, and 8 roots, respectively.

SIDE-OATS GRAMA

Just as the root-weight of big bluestem was much less in (5) Crete silty clay loam than in (4) Judson silt loam, so too the roots of side-oats grama were lighter in (16) Carrington silty clay loam than in the deep, rich (4) Judson soil (Fig. 30).

16. CARRINGTON SILTY CLAY LOAM, ROLLING PHASE

Hori-zon	Depth in.	Description
A_1	0- 7	Very dark gray (10YR 3/1 moist) silt loam; granular; pH 6.5
A_2	7-12	Dark gray (10YR 4/1 moist) silty clay loam; granular; pH 6.3
B_1	12-20	Very dark gray or dark grayish brown (10YR 3/1 to 10YR 4/2 moist) silty clay loam; blocky; pH 6.3
B_2	20-30	Dark grayish brown (2.5Y 4/2 moist) silty clay; blocky; pH 7.5

The lower inch is calcareous.

Increase in root-weight in (4) Judson soil at the several depths from the surface downward over that in (16) Carrington was 9.07, 0.54, 1.08, and 0.01 grams, respectively. Percentage distribution of weight was about the same in both soil types. Total root-weights were 28.3 and 39.0 grams, respectively.

KENTUCKY BLUEGRASS

Root-weight of Kentucky bluegrass was much the same and very small in both the upland (2) Carrington silty clay loam and in (3) Wabash silty clay loam of lowland (Table 2). But in (4) Judson silt loam with a 20-inch A horizon, roots in the first 6 inches were about 230 percent heavier. They averaged 112 percent heavier in the second 6 inches, and 300 percent in the second foot. While roots were confined to the first 2 feet in the first soil type and to 3 in the second, in Judson silt loam some extended into the fourth foot.

WESTERN WHEAT GRASS

Amount of roots of western wheat grass in the first 6 inches was about the same (approximately 10 gm.) in 3 of the 4 soil types in Table 3. But it was only 7.2 grams in the most compact soil, (8) Scott silty

TABLE 3. Distribution of root systems at each of the several depths and percentage of roots at each depth.

Spp.	Depth	5 Crete silty clay loam		6 Butler silt loam		8 Scott silty clay loam		9 Rendzina soil	
	in.	gm.	%	gm.	%	gm.	%	gm.	%
A sm[1]	0- 6	9.80	50.9	10.10	63.6	7.21	57.7	9.82	53.1
	6-12	2.71	14.1	1.48	9.3	1.65	13.2	3.11	16.8
	12-24	2.60	13.5	1.99	12.5	2.58	20.7	3.15	17.0
	24-36	2.34	12.1	2.31**	14.6	1.05	8.4	2.43	13.1
	36-48	1.81**	9.4						
	Total	19.26		15.88		12.49		18.51	

[1]A sm in *Agropyron smithii.*

clay loam. There was a very striking decrease in root-weight in the second 6 inches in the two soils—(6) Butler and (8) Scott—of the greatest compaction. Also the percentage of decrease in (5) Crete silty clay loam was approximately the same as that in the heavy but less compact (9) Rendzina soil. In the second foot the root-weight was about the same as that in the second 6-inch level in the (5) Crete silty clay loam and (9) Rendzina soil. But it was 34 and 56 percent greater in (6) Butler silt loam and (8) Scott silty clay loam, respectively. Root-weight decreased only a little in the third foot compared with that of the second in (5) Crete silty clay loam, but considerably in (9) Rendzina soil. There was a great decrease in weight in (8) Scott soil, where the root mass was only 31 inches deep, but in the deeper roots in the (6) Butler type it increased 16 percent over that of the second foot level.

Root-weight below the 0- to 6-inch layer was about the same in (5) Crete silty clay loam as in Sharpsburg silty clay loam a half mile distant where there was no claypan. Here the root-weight was somewhat less than in the Rendzina soil. But the Sharpsburg soil had been covered by two or more inches of dust which adversely affected the original prairie plants and permitted the entrance of wheat grass. Under this condition wheat grass developed extensive rhizomes which, with abundant stem-bases and a good

supply of surface roots, increased the weight in the surface 6 inches to more than twice that of either of the other samples.

Percentage of roots in the surface 6 inches was consistently low and often scarcely more than half of the entire root-weight. It varied from 50.9 to 63.6, being least in (5) Crete silty clay loam where the roots were longest. The Rendzina soil had the most roots at 6 to 12 inches (16.8 percent). The (8) Scott silty clay loam had the highest percentage of roots (20.7) in the second foot and also the lowest (8.4) in the third foot.

BLUE GRAMA

There is a striking decrease in the root-weight of blue grama at all levels in (11) Colby silt loam compared with that in (10) Hastings silt loam (Table 4). There is a 25 percent decrease in the weight of underground parts in the surface 6 inches and 28 percent in total root-weight. Weight decreases at 6-12 inches, and at 2, 3, and 4 feet are 48, 35, 37, and 24 percent, respectively. But even in the Colby soil there was a much better root development than in the very poor (2) Carrington silty clay loam at Lincoln. There the amount of plant material in the surface 6 inches was 41 percent less, and the entire root-weight only slightly more than half as great as in the Colby soil. The best development of roots was found in (4) Judson silt loam at Lincoln. Here the surface 6 inches contained 31.37 grams of roots compared with 22.55 in the (10) Hastings type and only 16.99 or a little more than half as much in (11) Colby soil. Total root-weights in the three soils were 35.76, 28.61, and 20.60 grams, respectively. But the root-weight in the Hastings type was greater at all depths below 6 inches, and sometimes twice as great as in (4) Judson silt loam. Thus, the increase in total weight of the root system was due to the concentration of material in the surface soil in the Judson type. Even the root-weight in Colby soil was greater in the third and fourth foot.

In the azonal soils of the loess, weight of roots of blue grama between 6 and 36 inches depth was 37 percent less than that of the same species growing in (10) Hastings silt loam. The heavy weight of the first 6 inches was a response to the darker and richer soil held in pedestals under the clumps. This soil was unusually well filled with roots and stem-bases. There was less root-weight in the other grasses which grew 5 or 6 inches lower on the eroding, less fertile soil.

Percentage of roots in loess soils at 0-6 inches was lowest in the best developed soil, (10) Hastings silt loam (78.8). It was higher in (11) Colby silt loam (82.5), and highest in the azonal soil of the loess (88.8). Conversely, the percentage of roots at any greater depth was highest in Hastings soil, less in Colby, but least in the azonal soil. Percentage of roots was the same (about 87.7) at 0-6 inches in (2) Carrington silty clay loam and (4) Judson silt loam at Lincoln, but it was greater at 6-12 inches in Carrington soil.

Table 4. Distribution of root systems at each of the several depths and percentage of roots at each depth.

Spp.	Depth	10 Hastings silt loam		11 Colby silt loam		Azonal soil		2 Carrington silty clay loam		4 Judson silt loam		Azonal soil (Sand dropseed)	
	in.	gm.	%	gm.	%	gm.	%	gm.	%	gm.	%	gm.	%
B gr[1]	0- 6	22.55	78.8	16.99	82.5	28.75	88.8	10.08	87.3	31.37	87.7	6.32	71.1
	6-12	2.80	9.8	1.47	7.1	1.99	6.1	.97	8.4	2.39	6.7	1.35	15.2
	12-24	2.05	7.2	1.34	6.5	1.49	4.6	.34	2.9	1.41	3.9	.78	8.8
	24-36	.92	3.2	.58	2.8	.17*	.5	.16	1.4	.45	1.3	.44*	4.9
	36-48	.29*	1.0	.22*	1.1					.14*	.4	(Sporobolus cryptandrus)	
	Total	28.61		20.60		32.40		11.55		35.76		8.89	

		12 Holdrege silt loam		13 Wabash silt loam (in Chernozem)		14 Sherman silt loam		Azonal soil				Azonal soil A sm	
B da	0- 6	15.12	70.6	17.09	69.7	18.56	68.6	7.79	64.7			6.37	56.3
	6-12	2.47	11.5	2.87	11.7	2.97	11.0	2.04	17.0			1.36	12.0
	12-24	2.39	11.2	2.63	10.7	3.21	11.9	1.75	14.5			2.09	18.5
	24-36	.78	3.7	1.28	5.2	1.29	4.8	.40	3.3			1.27	11.2
	36-48	.65*	3.0	.67*	2.7	1.00*	3.7	.06	.5			.23*	2.0
	Total	21.41		24.54		27.03		12.04				11.32	

[1]B gr is *Bouteloua gracilis* and B da, *Buchloe dactyloides.*

BUFFALO GRASS

Weight of roots of *Buchloe dactyloides* was greater at all depths in (13) Wabash silt loam, where there was a fill of 12 inches, than on the higher land where (12) Holdrege silt loam was sampled (Table 4). The increased weight was rather uniformly distributed throughout the root-length. Total root-weights were 24.54 and 21.41 grams, respectively. In (14) Sherman silt loam, with a buried profile where the sample was taken, total root-weight increased to 27.03 grams. This increased weight was only partly in the surface soil. At any depth the weight of roots exceeded that from either of the preceding monoliths. The greater weight in the second-foot level than at 6-12 inches is peculiar to this sample only and seems to reflect more favorable conditions for growth in the A horizon of the buried profile.

Weight of roots in the azonal soil varied from 12.04 grams in buffalo grass to 11.32 in western wheat grass, and was even less (8.89 grams) in sand dropseed. This is only half of the average weight of roots of the first two grasses where they grew in mature loess soils.

Percentage distribution of weight was remarkably uniform in the three soil types. Variations at 0-6 inches were from 68.6 to 70.6. They were even less in the second and third layers, but the (14) Sherman silt loam had the highest percentage of roots in the deeper soil (24 to 48 inches). Percentage of total root-weight in the azonal soil was much less (64.7) at 0-6 inches, but greater at 6-12 inches and in the second foot. A somewhat similar percentage distribution maintained in sand dropseed and in western wheat grass in the eroded soil. The greater weight of the second foot of wheat grass roots than the second 6 inches has been ascertained also in Sharpsburg silty clay loam.

PERCENTAGE OF ROOTS IN EACH MAJOR SOIL HORIZON

The percentage of the root system of big bluestem which occurred in the A horizon in the several soil types varied almost directly with its depth. As shown in Table 5, these percentages are in soil type (2) 0-7 inches, 78.0; (7) 0-11 inches, 75.9; (5, 1, and 15) 0-12 inches, 88.4 to 88.6; (3) 0-13 inches, 88.9; and (4) 0-20 inches, 89.8. Conversely, the percentage of roots in the B horizon decreased from soils with shallow A horizons to soils with deep A horizons. In the same sequence, the percentages are 18.3, 21.9, 11.5 to 7.2, 10.2, and 9.7. Roots in the C horizon decreased in the same general order—3.7, 2.2, 0.6 to 4.2, 0.9, and 0.5.

Proportion of the root-weight of little bluestem in the A horizon also varied with its depth, 84.6 percent where it was 11 inches deep (7), but 91.1 where it was an inch deeper (1). The deep B horizons contained nearly all of the remainder; (7) 11-36 inches, 14.3 percent and (1) 12-48 inches, 8.7 percent.

Switchgrass had 76.7 percent of its roots (to 5 feet) in the 12-inch A horizon, 21.2 in the 3-foot thick B horizon, but only 2.1 in horizon D.

Side-oats grama had 97.5 percent of the root-weight in the 20-inch thick A horizon of (4) Judson silt loam and the remainder in the thick B horizon. But in (16) Carrington soil the 12-inch A horizon contained 93.9 percent of the roots. The rest were distributed in the 8-inch B horizon (3.1 percent) and (3.0 percent) in the C layer.

Kentucky bluegrass in (2) Carrington silty clay

TABLE 5. Distribution of root systems of grasses in the several soil horizons. The depth of the A and B horizons and depth of the monolith in the C horizon are indicated in inches.

Spp.	H.	1 Sharpsburg silty clay loam			4 Judson silt loam			5 Crete silty clay loam			2 Carrington silty clay loam			3 Wabash silty clay loam			7 Crete silt loam		
		in.	gm.	%	in.	gm.	%	in.	gm.	%	in.	gm.	%	in.	gm.	%	in.	gm.	%
A fu	A	12	37.84	87.9	20	44.17	89.8	12	32.42	88.4	7	18.08	78.0	13	19.03	88.9	11	42.74	75.9
	B	48	4.96	11.5	53	4.79	9.7	28	3.07	8.4	22	4.24	18.3	36	2.18	10.2	36	12.34	21.9
	C	60	.27*	.6	60	.25*	.5	48	1.18*	3.2	48	.85	3.7	48	.19	.9	48	1.24*	2.2
A sc	A	12	47.34	91.1	*P vi / 1 Sharpsburg / silty clay loam*			12	43.88	76.7	*A fu / 15 Crete silty / clay loam*			12	59.12	88.6	11	50.28	84.6
	B	48	4.54	8.7				48	12.10	21.2				27	4.82	7.2	36	8.50	14.3
	C	60	.12	.2				60	1.20**	2.1				60	2.81*	4.2	48	.62	1.1
B cu	A				20	38.08	97.5							*16 Carrington / silty clay loam; / rolling phase*			12	26.60	93.9
	B				53	.96	2.5										20	.89	3.1
	C																41	.85	3.0
P pr	A				20	26.79	96.9				7	7.26	81.7	13	7.79	92.3			
	B				53	.87	3.1				22	1.63	18.3	36	.65	7.7			

loam had 81.7 percent of its roots in the 7-inch thick A horizon and the remainder in the B (7-22 in.) horizon. Where the A horizon was 13 inches deep (3, Wabash silty clay loam) 92.3 percent of the roots were in this layer and the remainder in the B horizon (13-36 in.). But as the A horizon became deeper (0-20 in. in 4, Judson silt loam) the percentage of roots in it increased to 96.9, some of the remaining roots penetrating the thick B layer (20-53 in.) to a depth of 4 feet.

Western wheat grass in the shallow A horizon (0-5 in.) of (8) Scott silty clay loam had the smallest percentage (55.2) of root materials (Table 6). The thickest A horizon (0-12 in.) in (5) Crete silty clay loam contained slightly less (65.0) than that of the shallower topsoil (7.5 in.) of the (6) Butler type. The B horizon of the Scott soil (5-41 in.) contained 44.8 percent of the entire root system, but that of the Butler (7.5-28 in.) only 24.7 percent, the remaining 8.1 percent occurring in the C horizon. Root distribution in Crete soil was somewhat similar to that in the Butler; the percentage in the B horizon (12-28 in.) was 18.4 and in the C, 16.6. Root distribution in the Rendzina was intermediate to that in the Scott and Butler soils. Percentage of roots in the B horizon was far greater than in any species of grass in the preceding, less compacted soils.

Percentage of roots of blue grama in the A horizon increased directly with the depth of this layer (Table 6). It was practically the same, however, in the

TABLE 6. Distribution of root systems of grasses in the several soil horizons. The depth of the A and B horizons and depth of the monolith in the C horizon are indicated in inches.

Spp.	H.	5 Crete silty clay loam			6 Butler silt loam			8 Scott silty clay loam			9 Rendzina soil		
		in.	gm.	%	in.	gm.	%	in.	gm.	%	in.	gm.	%
A sm	A	12	12.51	65.0	7.5	10.67	67.2	5	6.89	55.2	10	10.81	58.4
	B	28	3.55	18.4	28.0	3.93	24.7	41	5.60	44.8	27	5.93	32.0
	C	48	3.20**	16.6	36.0	1.28**	8.1	48			36	1.77	9.6

Spp.	H.	10 Hastings silt loam			11 Colby silt loam			2 Carrington silty clay loam			4 Judson silt loam		
B gr	A	15	26.04	91.0	12	18.46	89.6	7	10.30	89.2	20	34.86	97.5
	B	35	2.23	7.8	20	1.09	5.3	22	1.05	9.1	53	.90	2.5
	C	48	.34*	1.2	48	1.05*	5.1	36	.20	1.7			

Spp.	H.	12 Holdrege silt loam			13 Wabash silt loam (in Chernozem)				14 Sherman silt loam			
B da	A	12	17.59	82.2	Fill	12	19.96	81.4	A	17	23.31	89.5
	B	36	3.17	14.8	A	36	3.91	15.9	Old A	29	2.18	8.4
	C	48	.65*	3.0	C	48	.67*	2.7	B_1	36	.54*	2.1

12-inch thick horizon in (11) Colby silt loam and in the 7-inch layer of (2) Carrington silt loam. In both the amount was about 89.5 percent. In the surface 15 inches of (10) Hastings silt loam it increased slightly (to 91.0 percent) but the 20-inch-deep A horizon of (4) Judson silt loam contained 97.5 percent of the root-weight. From the 8-inch thick B horizon of (11) Colby silt loam, 5.3 percent of the root-weight was recovered. The 15-inch horizon of (2) Carrington silty clay loam had 9.1 percent. Conversely, the 20-inch thick B horizon of (10) Hastings silt loam had only 7.8 percent of root-weight, while the 33-inch B horizon of (4) Judson silt loam contained only 2.5 percent.

The percentages of roots of buffalo grass in the A, B, and C horizons are shown in Table 6 for (12) Holdrege silt loam only. The (14) Sherman silt loam contains a buried soil; the Wabash silt loam has a 12-inch fill. Regardless of these, the upper layer in each soil which is 12 inches thick contains about 82 percent of the root system; the 17-inch A horizon 89.5. Likewise, the deeper second layers have more roots (14.8 to 15.9 percent) than the shallower one in (14) Sherman silt loam which has 8.4 percent.

DISCUSSION

The well drained and well developed "zonal" soils of the grasslands of Nebraska and Kansas comprise chiefly three great groups—the black "Prairie soils" of the humid grasslands, the "Chernozems" ("black earths") of the subhumid grasslands, and the "Chestnut" (Dark-Brown) soils of the semiarid grasslands. The still lighter colored "Brown soils" occupy only a small total area in southwestern Kansas. Associated with each of the zonal soils are other soils, some young ones with only the beginnings of soil development (azonal soils), some with excessively developed claypan subsoils (Planosols), and others poorly drained and marshy but without claypans (Wiesenboden) of the intrazonal order.

Samples of zonal soils taken near Lincoln are from the boundary between the zones of Prairie and Chernozem soils. Prairie soils typically are nearly black, moderately to strongly acid in reaction, and without an accumulation of calcium (lime) carbonate in the subsoil. The Chernozems are similar to the Prairie soils in color but are nearly neutral in reaction and typically have an accumulation of lime carbonate in their subsoils. Chestnut soils are somewhat lighter-colored and lower in organic matter than the Chernozems.

Soils generally grade into one another without sharp breaks. Hence, some of the samples described in this paper are intermediate between types rather than representing the mode for each type. This caused some difficulty in classifying some of the soils.

Roots were not separated in the surface soil principally because the rhizomes and stem-bases function as roots in the processes of modifying soil structure, adding organic matter to the soil, and in preventing erosion. They are produced at about the same general rate as roots and are no more nor no less resistant to decay than are the absorbing organs (Weaver & Zink 1946; Weaver 1947). Soil scientists were in agreement with the authors in their decision not to exclude the underground stems and stem-bases from the materials in the topsoil.

It is of interest, however, that the roots alone often constitute the minor part of the weight of underground materials in the surface soil. In one determination on about 3 square feet of each of three species, the roots of big bluestem composed 49.5 percent of the weight of plant materials in the surface 4 inches of soil. Likewise, they composed only 28 percent in both little bluestem and blue grama. Despite this, in big bluestem 43 percent of the entire root system by weight was found in the surface 4 inches of sod after three growing seasons. In little bluestem it was 36 percent, and in blue grama 49. The first foot of soil contained 78 percent of the roots of big bluestem, 69 percent of little bluestem, and 80 percent of the roots of blue grama (Weaver & Zink 1946).

The 33 monoliths examined were taken in three general areas. One was in the vicinity of Lincoln near the Prairie soil-Chernozem border in eastern Nebraska. A second was 65 to 125 miles southwestward in the Chernozem soil area at Carleton and Bruning, Nebraska, and Belleville, Kansas. The loess hills near Kearney in central Nebraska, also in the general Chernozem soil area, was the source of the third group.

Each monolith was taken for some special reason. The study of big bluestem in many different soils was chiefly due to the fact that since the death by drought of more than 90 percent of little bluestem in eastern Nebraska, big bluestem is the most widely represented predrought dominant of true prairie. An early excavation of both these species in the soil of a single trench (1, Sharpsburg silty clay loam) was for the purpose of a careful comparison of the two root systems.

Further study of big bluestem revealed a reason for its spreading into most soil types of upland as well as lowland. The coarse, deep, but comparatively poorly branched root system typical of deep, well watered, and fertile soils as (7) Crete silt loam (thick solum) and (4) Judson silt loam was greatly modified in less mesic sites. Here the main roots were usually much finer and much better branched, and somewhat more of the root-weight occurred near the surface of the soil. These adjustments of this plastic root system help explain the wide postdrought distribution of this grass, sometimes in somewhat droughty soils like (2) Carrington silty clay loam. But where native vegetation on uplands was kept thinned by repeated deposits of dust (15, Crete silty clay loam), and there was much available space from which to obtain both water and nutrients, a deeper, coarser root system was again maintained.

The root system of little bluestem was much better developed in (7) Crete silt loam with a thick solum than in a semiupland site (1, Sharpsburg silty clay loam). The root system from a third monolith of an
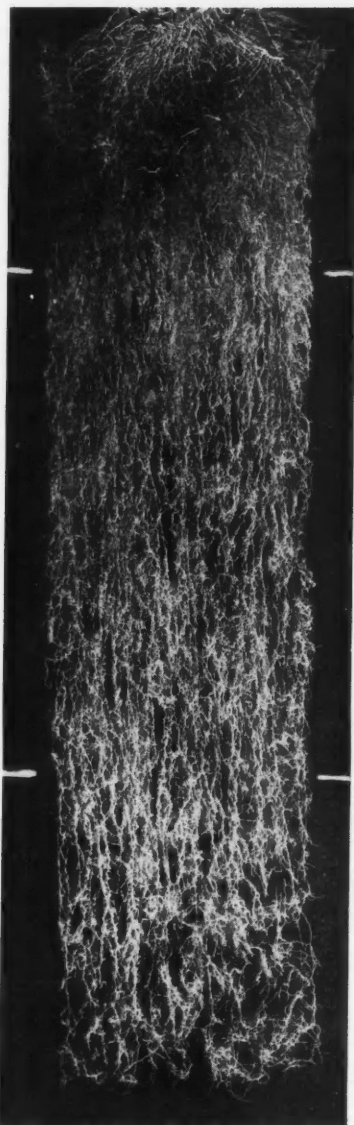
Fig. 31. Root system of little bluestem from a 4-foot monolith of Carrington silty clay loam. The A horizon was 12 inches thick. This dense, well-branched root system is very uniform in appearance throughout the B horizon (12 to 34 in.). Many roots extended more than a foot below the solum into the parent material.

upland soil (Carrington silty clay loam), not weighed but mounted for class use, had finer but more profusely branched roots than either of the preceding (compare Fig. 31 with 1 and 15). Similar differences were found in the roots of blue grama and Kentucky bluegrass (Table 2).

The great invasion of western wheat grass and its almost complete replacement of other native vegeta-

tion over vast areas of prairie and pasture occurred during the cycle of drought (1934-40). The difficulty of its replacement by other species and consequently its persistence in many places in pure stands is a problem of great economic importance. Wheat grass lacks the dense mass of fine leaves characteristic of bluestems and most other prairie grasses. Hence, it permits the beating rains to destroy the soft crumb-like soil aggregates at the surface. Rapid penetration of water is prevented by puddling of surface soil. Consequently the soil absorbs less of the precipitation, runoff is promoted, and erosion is accelerated. As a result, conditions of drought have been maintained for a long period of time.

Before the drought, western wheat grass was confined largely to certain clay soils and soils with clay-pans. It now covers many "slick spots" as well as other soils. The root distribution was studied particularly to obtain further information on this problem. It appears now that replacement of wheat grass by more mesic species is occurring gradually on soils that have not degenerated into Planosols, but that wheat grass may persist for a long time or indefinitely where heavy claypans are present.

In the loess hills of central Nebraska a chief type of natural vegetation is short grass. Under grazing this community becomes more and more widely spread and finally excludes all others. Studies on yield and consumption of blue grama and buffalo grass prompted a study of the root system in the various soil types from the light-colored (11) Colby silt loam to the darker (13) Wabash silt loam in the valleys. The effect of extensive erosion of these relatively unstable soils, brought about by overuse of the range or plowing and abandoning the land, was shown everywhere. Root distribution in the resulting azonal soils aided in understanding the decreased yield and the slow development of a new cover of vegetation. This required a number of monoliths besides those in the short grass.

The problem of a buried soil profile and its effect upon root distribution is intriguing. Such profiles occur in many places and often account for abrupt differences in the composition of the vegetation and are definitely known to affect root habits within the species as well. For example, the Loveland loess accumulated rapidly as a thick cover over the region in central Nebraska now known as the Loess Hills and Plains. Its deposition was followed by a relatively long period of weathering and soil development. Thus a dark surface soil with a reddish brown clayey subsoil was developed at the top of the Loveland. This differs greatly in texture and permeability not only from the coarse silt of the middle and lower parts of this loess but also from the lower and middle parts of the yellowish to whitish Peorian loess which was deposited upon a rough topography during later periods of loess accumulation. Under these conditions water from precipitation tends to move downward, 30 to 40 feet where the layer of Peorian loess is thick, with comparative ease until the Peorian-

Loveland contact is reached. Here permeability is greatly restricted and the groundwater movement is directed laterally toward the valley or canyon sides where it is discharged as seeps or springs. Thus grasses growing on a hillside in soil originating from a thin layer of Peorian loess may extend their roots into the topsoil of the Loveland. Deeper roots, as those of *Liatris punctata, Rosa pratincola,* or *Lygodesmia juncea,* may make these contacts at a depth of 10 to 20 feet. The differences in soil compaction, water content, and amount of clay and nutrients, often cause marked differences in root development. Such differences were shown in a small degree by buffalo grass in (14) Sherman silt loam. (See also the grass roots in (2) Carrington silty clay loam.)

Future studies should include chemical analyses of the soil especially in the subhorizons where marked differences in root numbers or branching occur. Water relations and air content of soils at various depths during the growing season, especially in claypan soils, should be ascertained. Perhaps the shorter-lived roots of annual cereal crops react quite differently than those of perennial grasses and tend to develop mostly on the surfaces of the prisms and blocky soil structures. A monolith with a large portion of a well established root system lends itself readily to experimentation on the absorbing capabilities of roots at various levels. When the monolith is taken in an appropriate box, nutrients may be added at any level. Or after the soil and plants have dried and the tops are dead, the degree of new growth from water applied directly at different levels yields information on amount of absorption at different depths. Preliminary studies on the growth of grasses when watered at various depths show that roots absorbing water at a depth of 2 or even 3.5 feet only, produced only a small amount of tops. The amount of absorption decreased directly with the depth at which the soil was supplied with water (Nedrow 1937).

This method is applicable in the study of the soil-root relationships not only of introduced grasses, weedy grasses, and cultivated cereals, but also to many non-grassy species of native and crop plants. The monoliths might be widened and deepened if necessary. The general spreading and depth of roots in all the species here recorded may be found in the early literature already cited.

SUMMARY

A new method has been devised for obtaining representative samples of entire root systems. It permits the studying of the intimate relations of roots and soils, and of measuring root production quantitatively at various soil levels.

Descriptions have been made of each of 16 soil types from which 11 species of grasses were taken. They include not only the depths of the main soil horizons and the minor subdivisions of each, but also the color, texture, structure, consistence and pH of soil in each subdivision. Some interrelationships of the soil types are given.

Monoliths of soil 12 inches wide, 3 inches thick, and from 3 to 5 feet in depth were taken from the walls of trenches made in selected pure stands of each species. The 33 monoliths examined were taken in three general areas. One was in the vicinity of Lincoln near the Prairie soil-Chernozem boundary in eastern Nebraska. Another was 65 to 125 miles southwestward in the Chernozem soil area, and the third in the loess hills near Kearney in central Nebraska where both Chernozem and Dark-Brown soils are found.

Roots were obtained from the monolith by a sytsem of soaking and gentle washing. A special technique was used in mounting; lighting for photographing was by electro-flash units, and sectioning was done in such a manner as to obtain the oven-dry weight for each 6 inches or foot in depth as well as for each major horizon.

Kentucky bluegrass *(Poa pratensis),* blue grama *(Bouteloua gracilis),* and big bluestem *(Andropogon furcatus)* were studied in a shallow, compact Carrington silty clay loam, in a young, alluvial Wabash silty clay loam, and in deep, well drained Judson silt loam developed in silty colluvium, a soil type lying between upland soils and alluvial bottomlands. The roots of bluegrass increased in depth from 22 to 36 inches and then to 48 from Carrington to Judson soil type. The bulk of the roots (82 percent) were confined to the shallow A horizon (0-7 in.) in the first type. In the second, the massive portion of the root system was slightly less dense but extended more deeply. In Judson soil the deep A horizon (0-20 in.) was filled with a great mass of roots with a total weight more than three times as great as either of the preceding root systems.

Blue grama developed 89 percent of its roots in the shallow A horizon of the Carrington silty clay loam. In the Judson silt loam a great mass of roots grew in the A horizon and extended through the B1 (20-31 in.) as well. The ratio of the weight of the first root system to the second was 1 to 3.

The normally deep-rooted big bluestem extended only a few of its roots beyond 3 feet in depth in both the Carrington and Wabash soil types. Chief differences were a denser mat of roots in the A horizon and much finer roots with more numerous branches in Carrington soil. The mass of roots penetrated only half as deeply here as in Wabash soil. The dense root system in the A horizon of the Judson soil weighed approximately twice as much as either of the preceding entire root systems. Root depth was 5 feet.

Five monoliths were taken, all with western wheat grass *(Agropyron smithii),* from intrazonal soils in Prairie and Chernozem areas. The claypan (B horizon) in Crete silty clay loam at Lincoln was at 12-28 inches depth. Roots were abundant, well branched, and easily washed from the mellow, granular topsoil. The blocky prismatic, compacted soil of the B layer was less well penetrated by roots; it was removed with difficulty. Greatest branching and a large proportion of the root system occurred below 28 inches in the mellow, loessal parent material of the C horizon.

Butler silt loam in the Chernozem area had a 7.5-inch A horizon. The dark colored B horizon (7.5-28 in.) of blocky clay was a barrier to the penetration of both water and roots, at least when dry, except the deep cracks caused by shrinkage during drought. Only in the lower third of the B and especially in the yellowish, less compact C horizon was branching of roots pronounced. Weight of roots in the 13 inches below the level where good branching began was 36.5 percent greater than in the 13 inches above. This deeper soil apparently received much water through the cracks in the claypan.

Fifty feet distant from the trench in Butler soil, roots of the bluestems were examined in monoliths of Crete silt loam with a thick solum. Here root distribution was quite unlike that of wheat grass. Roots were much heavier, their weight decreased uniformly with depth, and they occupied the soil, which was far more uniform in structure, to a depth of 4 to 4.5 feet.

A distribution of roots similar to that in Butler soil occurred in Scott silty clay loam, only here the claypan at 5 to 41 inches was thicker and even more compact. No roots extended beyond 31 inches, except in deep cracks. Roots penetrated the prisms and blocks of soil (probably when these were moist) which were so hard when dry that they could scarcely be crushed with a sledge hammer. Many branches were short, flattened, and thickened.

A 38-inch deep, well drained Rendzina soil with a clayey subsoil overlaid hard, unweathered limestone. Here the distribution of roots was similar to that in soils with a claypan; 42 percent were below the 10-inch A horizon.

Blue grama was examined in a monolith taken on a loess hill near Kearney in a mature soil, Hastings silt loam. Roots were especially abundant in the A horizon (0-15 in.) but fewer at greater depths. They continued to branch profusely to 4 feet; a few were 5 feet long. But in the immature Colby silt loam in a similar site, although the roots were concentrated in the 12-inch A horizon, even this layer was relatively poorly occupied. Root-weight was 25 percent less at 0-6 inches depth here than in Hastings soil. Differences at greater depths were even more marked, but depth of penetration was 5.5 feet.

Buffalo grass (Buchloe dactyloides) in a mature loess soil, Holdrege silt loam, on upland was remarkably uniform in decrease of roots with depth; some roots were 6 feet long. In a flat-bottomed valley of Wabash silt loam the roots were heavier at all depths than in Holdrege soil; some were 6.5 feet deep.

In Sherman silt loam on a hillside where there was a buried soil profile at 17 inches depth, the root system of buffalo grass was somewhat better developed at all levels than either of the preceding. Unlike roots in the preceding soil types in loess, which decreased in weight with depth, here there was an increase in weight in the second foot over that in the second 6 inches, probably due to the buried A horizon of an old soil.

In much eroded loess where the entire solum had been removed, development of several grasses was only about half normal. Root systems of buffalo grass, western wheat grass, and sand dropseed (Sporobolus cryptandrus) weighed only about half as much as roots of the same species in mature Holdrege silt loam. The root mass was concentrated in the upper 12 inches; a 2- to 3-inch A_1 horizon was developing.

Weight of roots of big bluestem at 0-6 inches depth ranged from 16.8 to 53.5 grams in the different types of soil. These amounts were 79 and 80 percent, respectively, of the total root weight. In the second 6 inches the range was from 2.0 to 8.2 grams. Roots in the second foot always weighed less than those in the second 6 inches, just as root-weight in the third foot was always less than that in the second. No plant produced more than 1.24 grams of roots in the fourth foot.

Percentage of roots of big bluestem in the surface 6 inches ranged from 75.3 to 80.2 in the three soil types of upland and much less (63.5 to 78.7) in four soil types on lowland. Percentage of roots in the second 6 inches and in the second foot was lower in upland types.

Total root-weight and distribution of root-weight of little bluestem (Andropogon scoparius) were not greatly different from those of big bluestem, except the roots were heavier in the surface soil and the root system was 12 to 18 inches shallower. Total root weight of side-oats grama (Bouteloua curtipendula) varied from 28.3 grams in Carrington silty clay loam to 39.0 in Judson silt loam but percentage distribution of weight was about the same in both soil types.

Roots of bluegrass varied in weight in the surface 6 inches from 6.78 grams in Carrington silty clay loam to 22.04 in Judson silt loam. Total root-weights were 8.89 and 27.66 grams, respectively.

Weight of roots of western wheat grass was low, 7.21 to 10.10 grams in the surface 6 inches of all the claypan soils. Percentage of root-weight here was also consistently low and often scarcely more than half that of the entire root-weight. There was a striking decrease in weight (to 1.48 and 1.65 grams, respectively) in the second 6 inches in the two soil types (Butler and Scott) of greatest compaction. Weight increased 16 percent in the third foot of Butler soil over that of the second foot.

Roots of blue grama in the upper 6 inches of Colby silt loam were 25 percent lighter, and the total root-weight was 28 percent less than in Hastings silt loam. Likewise root-weight in Carrington silt loam at Lincoln was 41 percent less in the surface 6 inches and total root-weight was only about half that in Colby soil. The heaviest root system was in Judson silt loam, 35.76 grams, compared with 28.61 in Hastings soil, 20.60 in Colby, and 11.55 in Carrington.

Greater root-weight of buffalo grass at all depths was obtained in Wabash silt loam (at Kearney) than in the higher land where Holdrege silt loam was sampled. Total root-weights were 24.54 and 21.41 grams. But in Sherman silt loam, root-weight exceeded that from either of the preceding monoliths at all depths.

Root-weights of buffalo grass and western wheat

grass in azonal soils of loess were reduced to 12.04 and 11.32 grams respectively, which was about half their weights in mature loess soil, as Holdrege silt loam.

Percentage distribution of weight of roots of buffalo grass was remarkably uniform in the three soil types in loess. Variations were from 68.6 to 70.6 percent at 0 to 6 inches and even less in the second- and third-foot depths.

Percentage of roots of big bluestem in the A horizon of the several soil types varied almost directly with its depth from 78.0 in a 7-in. horizon to 89.8 in one 20 inches deep. A similar relationship was found in both little bluestem and side-oats grama. In bluegrass the percentages were 81.7, 92.3, and 96.9 in A horizons 7, 13, and 20 inches deep, respectively.

Western wheat grass in the shallowest (0-5 in.) A horizon had the smallest percentage of roots (55.2). In the deepest (0-12 in.) the root-weight was 65.0 percent.

Percentage of roots of blue grama in the A horizon increased directly with the depth of this layer from 89.2 (0-7 in.) to 97.5 (0-20 in.).

Regardless of a 12-inch fill in Wabash silt loam this layer had nearly the same percentage of roots of buffalo grass (81.4) as the 12-inch A horizon of Holdrege silt loam. But the deeper A horizon (0-17 in.) in Sherman silt loam contained 89.5 percent of the entire root system.

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STUDIES ON THE BIOLOGY OF THE EDIBLE OYSTER, *OSTREA RHIZOPHORAE* GUILDING, IN PUERTO RICO

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STUDIES ON THE BIOLOGY OF THE EDIBLE OYSTER, *OSTREA RHIZOPHORAE* GUILDING, IN PUERTO RICO

INTRODUCTION

Much has been written on the biology of the edible oysters, especially *Ostrea virginica* (Gmelin), but to the best of the writer's knowledge very little has been written on the biology of these animals in tropical environments. When this present work was begun in the fall of 1946 it was with the idea that the oysters being studied were *O. virginica* (Mattox 1948). However, as additional information was gathered in regard to the biology of oysters living in the waters around Puerto Rico, it became apparent that these forms differed in many respects from *O. virginica* as found in the North American waters.

The edible oysters of Puerto Rico were first referred to as *Ostrea parasitica* Gmelin by Stahl (1882). Dall and Simpson (1902) used the name *O. virginica* (Gmelin) for these animals. Since that time specimens of these animals from Puerto Rico have been referred to under this name in the various museum collections. However, Lamy (1929) working on the lamellibranchs of Martinique pointed out that the oysters of that area, living on the roots of the common mangrove, *Rhizophora mangle* Linn., should be placed under the name *Ostrea rhizophorae* Guilding, described from a lagoon on Carriacou Island of the Grenadine group. Lamy also indicated that the name *O. parasitica* Gmelin was the valid name for an Indian Ocean oyster and should not be applied to the West Indies form. Reeve (1871) figures *O. rhizophorae* as the form typical of the Caribbean area. McLean (1941) pointed out that *O. rhizophorae* is known from Cuba and the West Indies, but no specific mention was made of the species found in Puerto Rico.

Ostrea rhizophorae is very similar in form to *O. virginica*. However, there are differences, as pointed out by Guilding (1828) and Reeve (1871). The inferior, left, valve of *rhizophorae* is not as plicated as in *virginica*. Also the inferior valve is very concave and the right valve very flat. The muscle scar is more rounded and in most individuals there is a complete absence of color or only a very faint blue color and not the dark purple that is characteristic of the muscle scar of *O. virginica*. Also the teeth are not well developed on each side of the hinge of these forms as in *virginica*. The shell is thin, foliaceous, and marked with irregular purple stripes. Based on the observations reported here *rhizophorae* does not reach the large size attained by *virginica*. Other biological differences are discussed elsewhere in this paper.

Preliminary observations showed that most of the colonies of oysters in the waters around Puerto Rico are found in inlet lagoons that are nearly cut off from open water, lagoons in which there is very little circulation of the water with open bays or the sea. The oysters are found living attached to the aerial roots of the common mangrove, *Rhizophora mangle* Linn., which surrounds these lagoons. This habit of growth gives these oysters their common name, "the mangrove oyster." The largest and most important colonies are found on the Caribbean side of the island. Colonies of importance are found at Puerto Real, Boqueron, Parguera, Salinas, Ensenada Honda and a small one at Arecibo (Fig. 1). Of these colonies the one of greatest commercial importance is found in "Laguna Rincón," off the Bay of Boqueron.
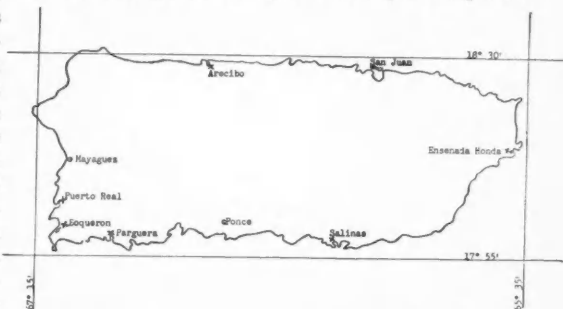

Fig. 1. Outline map of Puerto Rico indicating the location of the larger colonies of *Ostrea rhizophorae*.

This lagoon at Boqueron is located almost exactly on the 18° north latitude parallel and 67° 10′ west longitude meridian. It is here in this lagoon that the writer has carried on this series of observations. Transportation problems have limited short interval or continuous observations. However, the writer feels that the data gathered from the 2 to 4 week interval collections are representative, show the normal variations and are sufficiently significant.

The Boqueron lagoon is approximately 1½ miles long at its greatest length and near ½ mile wide at its greatest width at the eastern end of the area (Fig. 2). The canal which forms the connection with the open Bay of Boqueron is about 50 yards wide and 200 yards long. The entire lagoon is completely surrounded by mangroves. Oysters are found living on the roots around the entire circumference, attached to the roots within the very narrow, 1 to 2 feet, intertidal zone. However, the greatest concentration of the oysters is on the northwestern side of the lagoon.
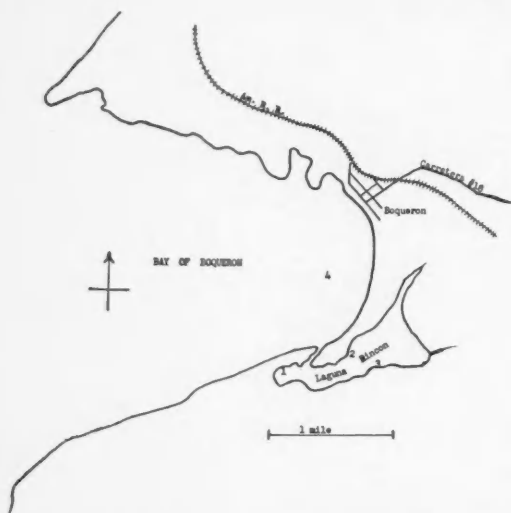
Fig. 2. Detailed map of the area at Boqueron Bay showing the lagoon, "Laguna Rincón," where this study was carried on.

One of the factors envolved in this distribution of the oysters is probably the prevailing winds that blow from an east by southeast direction which results in a prevailing wave action on the west and north-western sides of the lagoon. Other factors envolved in this distribution will be discussed later.

It should be pointed out here that this colony of oysters is of local commercial importance. Obviously it does not approach the well known oyster beds of the Atlantic and Gulf coasts of the United States, but nevertheless is of significant local importance. From reliable sources it is estimated that an average of 4,000 oysters, of market size, are gathered from this lagoon every week throughout the entire year. Some weeks as many as 10,000 oysters are taken from this lagoon. The total numbers taken during one year would thus be near 250,000 oysters or roughly 25,000 lbs. of oysters, based on an average taken from a group picked for the market. This quantity of oysters would sell on the local markets in Puerto Rico, principally San Juan, Ponce and Mayaguez, for nearly $5,000.00.

Even though the fishermen attempt to collect only the larger oysters for the market many small individuals are taken with the large ones. This is due to the method of growth which results in the attachment of the spats to the shells of older oysters and hence the gathering of the small with the large oysters. The writer examined closely a collection of oysters that were sold as 100 oysters for table use. In this group there were 103 oysters of a shell length greater than 45mm., a size below which the oysters are too small to be considered of table size. The average size of these 103 was near 57mm. with the largest measuring 79.8mm. With these 102 there were 109 oysters that ranged from 4.1mm. up to

44mm. with an average of 25mm. in shell length. In another such collection of 100 market size oysters there were 145 oysters, 40mm. or under in size, attached to the shells of the larger individuals. Such a system of collection obviously is not an economical one so far as maintaining the colony is concerned.

Since such collecting methods in an area of this size in the Atlantic or Gulf coast oyster beds would soon deplete the colonies, and since the colony here at Boqueron does not seem to be decreasing in relative size, a series of investigations were undertaken to determine differences between this colony and those found in the temperate zone. Both physical and biological factors have been studied.

At this time the writer wishes to express his gratitude for the cooperation of the officials of the College of Agriculture and Mechanic Arts, University of Puerto Rico, at Mayaguez, Puerto Rico, where this work was carried on, for their aid in providing transportation and laboratory facilities. The cooperation of the fishermen at Boqueron is also appreciated. These men made available small boats from which all field study was carried on, and also they provided valuable information in regard to their commercial oyster activities. Also the writer was permitted use of the laboratory of the Mayaguez Station of the U. S. Bureau of Fisheries and Wild Life Service, which was greatly appreciated. The writer wishes to acknowledge the assistance given by Prof. José A. Ramos in making the photographic records used here, also the generosity of Dr. Willis G. Hewatt in assisting with the plankton counts.

HYDROGRAPHIC OBSERVATIONS

In order to make a comparative study of the various factors that may influence the distribution and growth of the oysters in the lagoon at Boqueron, the writer set up a number of study points, stations, in the lagoon (Fig. 2). At each station temperature, salinity, pH, and dissolved oxygen records have been made. Stations 1, 2, and 3 are considered here as representative and significant. Station 2 is located near the center of the area most heavily populated by oysters and Station 3 in an area of lightest concentration. Records of the physical factors were also made from near the center of the Bay of Boqueron, Station 4, to be used as a comparison for conditions existing in the lagoon.

The water within the lagoon is turbid throughout most of the year. This is partially due to the prevailing winds which blow toward Stations 1 and 2, as previously indicated. The turbidity is also due to the fact that the bottom of the lagoon is of a very fine mud and silt over most of its extent. Through the open central water of the lagoon much of the bottom has a heavy growth of "turtle grass," *Thalassia testudinum*. This alga does not grow along the semi-shaded edges, shaded by the mangrove trees on the aerial roots of which the oysters attach. The mud bottom thus restricts the distribution of the oysters by silt-covering any solid objects that might be on the bottom. The turbidity and silt also help account for

the distribution of the oysters in the upper level of the intertidal zone. The water in the lagoon is very shallow, averaging only about 3 feet in depth at low tide.

On the basis of comparative physical factors, discussed later, it is the writer's opinion that there is no important tidal change in the lagoon so far as the main mass of the water is concerned. There is obviously some change but complete freshening of the lagoon from the open bay does not seem to occur. Also it should be pointed out that very little fresh water, from rains, enters the lagoon. Boqueron is in a relatively dry region, 20 to 40 inches annual rain fall, and there are no permanent streams entering the lagoon. The fresh water that does enter the lagoon, from the eastern and southern sides, is from drainage ditches which flow only after the heavy spring rains.

TEMPERATURE

Much has been written in regard to the influence of temperature on the various life activities of oysters, especially on spawning and feeding. Various temperatures have been given as "critical" temperatures for spawning (Churchill 1920, Gutsell 1924, Nelson 1928, Prytherch 1929, Hopkins 1931, 1936, 1937, Orton 1920, Loosanoff & Engle 1940, Galtsoff 1930, 1932) temperatures varying from 8°C. for *O. gigas* (Hopkins 1936) to 25°C. for *O. virginica* (Hopkins 1931). Physiological races have been postulated by Stauber (1947) on the basis of the critical temperatures in different localities at which *O. virginica* spawns. As will be pointed out later, there is apparently no critical temperature for spawning of the oysters found at Boqueron as spawning seems to take place throughout the entire year.

As would be expected the water temperature at 18° north latitude varies very little. During the course of observing the water temperatures from November 1946 to May 1948 the lowest average temperature for all stations was 25.5°C. taken on January 12, 1947 and March 2, 1948 (Fig. 3). The highest average temperature was 30.5°C., observed August 22, 1947.

Temperature readings were made within the upper 12 inches since that is the region in which most of the oysters are found living. As indicated in Figure 4, the variations in temperature at the different stations are negligible. Both the lowest (25.0°C.) and the highest (31.0°C.) temperatures were recorded at Station 2. The low point was probably due to wind and wave action and the highest because of the direction of the sun. The temperatures of the surface waters of the open bay varied very little from those of the lagoon. The relatively uniform warm water here is probably a factor which is responsible for the rapid growth of the oysters, as will be pointed out later.

DISSOLVED OXYGEN

In an effort to determine physical factors which might influence the distribution of the oyster in the lagoon a series of dissolved oxygen tests were made. Water samples were taken in standard sample bottles and the Rideal-Stewart modification of the Winkler Method was used for the determinations.

The fluctuations in parts of O_2 per mille followed the expected course in relation to the temperature changes (Fig. 3). The lowest average concentrations for the lagoon were recorded where temperature averages were 30.0°C., these were 3.9⁰/oo September 30, 1947 and 3.5⁰/oo May 25, 1948 (the latter followed a period of prolonged hot and dry weather). The
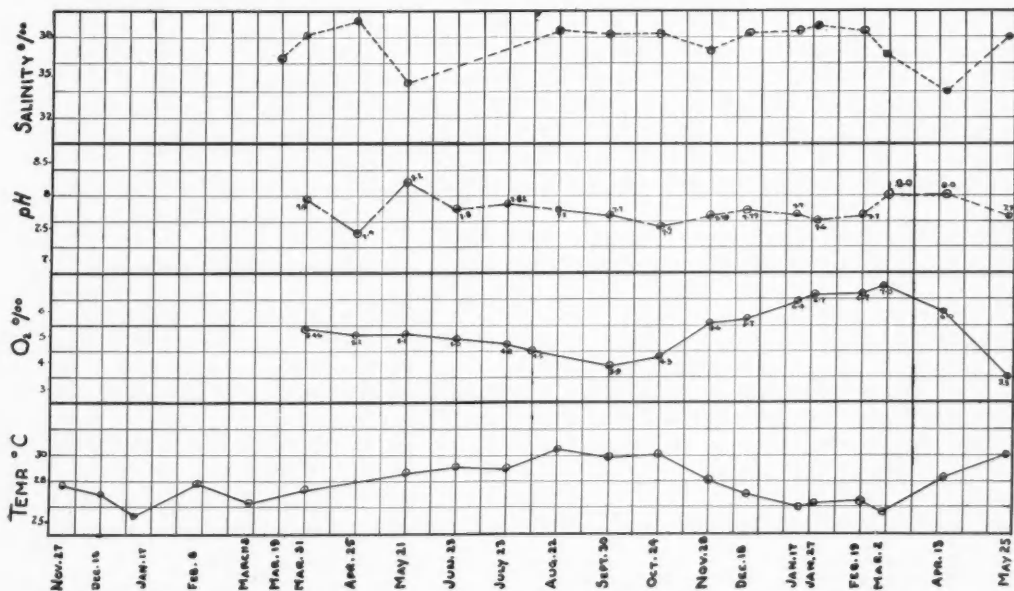

FIG. 3. A summary of the average temperatures, oxygen, salinity, and pH readings for all of the stations.
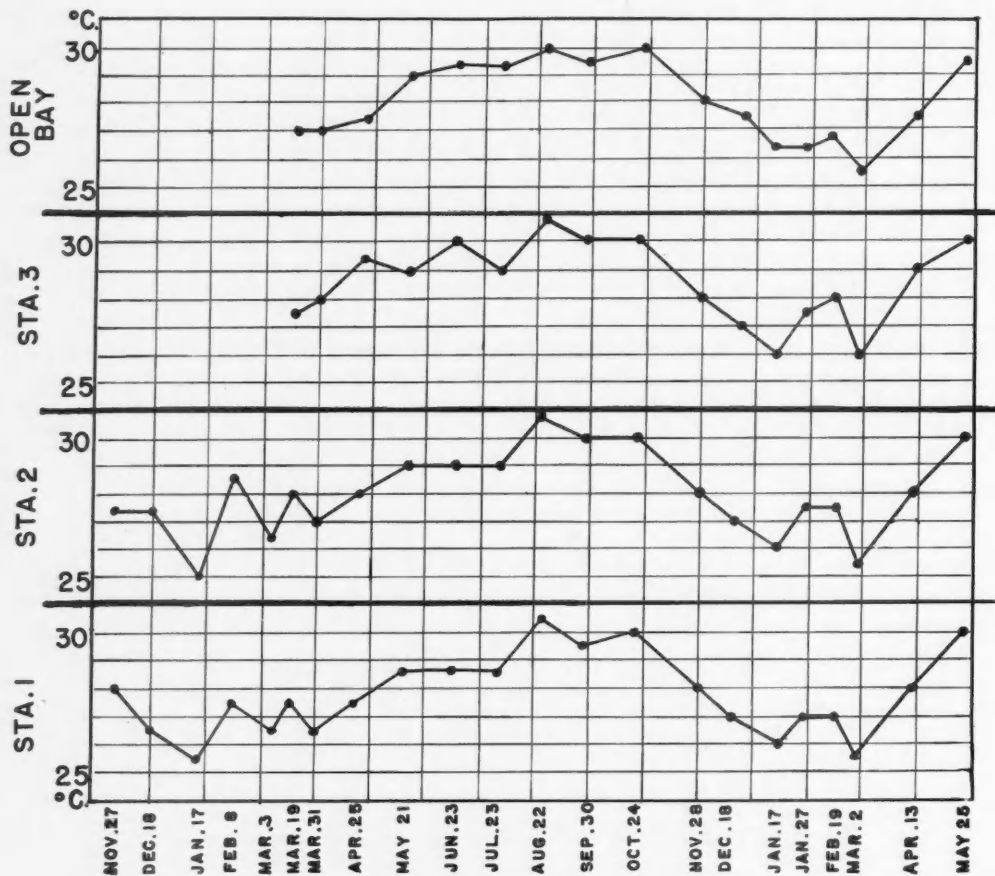
Fig. 4. Temperature variations for the different Stations at Boqueron.

highest average concentrations occurred after an un-
usually cool period, March 2, 1948 when the concen-
tration was 7.0⁰/oo. When dissolved oxygen con-
centration of the various stations in the lagoon are
compared with those of the open bay (Station 4, Fig.
2) it is seen that the bay waters consistently con-
tained more oxygen.

As is shown in Figure 5, Stations 1 and 2 were
more consistently near the oxygen content of the open
bay than Station 3. At Station 3 the oxygen parts
per mille were always lower than the other stations,
ranging from 3⁰/oo to 6.5⁰/oo in contrast to the
4⁰/oo to 7.7⁰/oo at Station 1. The lower oxygen
content may be part of the explanation for fewer oys-
ters at this station, probably it is a part of a group
of restricting factors as will be pointed out later.

HYDROGEN-ION CONCENTRATION

Studies by Hopkins (1931) in Galveston Bay,
Texas, where high temperatures are encountered, indi-
cated a characteristic pH of the water between 8.0
and 8.4. Loosanoff & Engle (1940) indicated a rather

uniform pH for Long Island Sound at 8.0 to 8.3.
These workers indicated a lower pH, 7.1, after heavy
rainfall, hence lower salinity.

In the lagoon at Boqueron where 16 readings were
taken, with a Beckman indicator, over a period of
over a year the average pH was 7.75. The average
pH readings for all of the stations ranged from 7.4
to 8.2. Here too the rainy seasons, with accompany-
ing salinity changes, resulted in pH changes. How-
ever, with a lower salinity here the pH was higher,
as is indicated in Figure 3 for May 21, 1947, when
the pH was 8.2, and again during the spring rains
of 1948 when the pH was up to 8.0 in March and
April. Figure 6 shows the pH range for the different
stations. As is seen the fluctuations at Stations 1 and
2 are less than those at Station 3 where the pH read-
ings were in general lower than elsewhere. It was
noted that the pH in the open bay was generally
higher than in the lagoon, the average here was
nearer 8. In the writer's opinion there probably is
no significance in the lower pH found here with
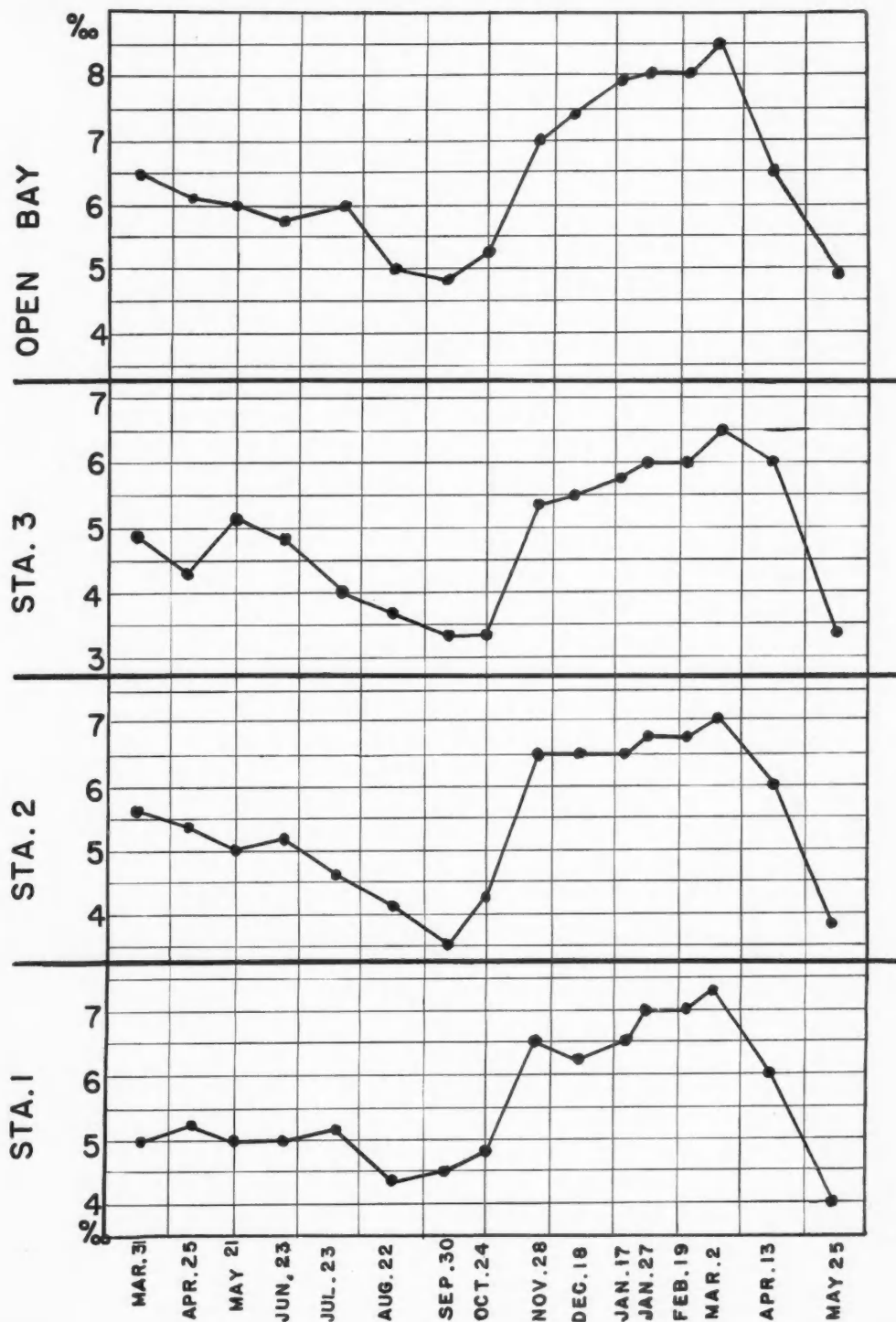regard to the ecology of these oysters.

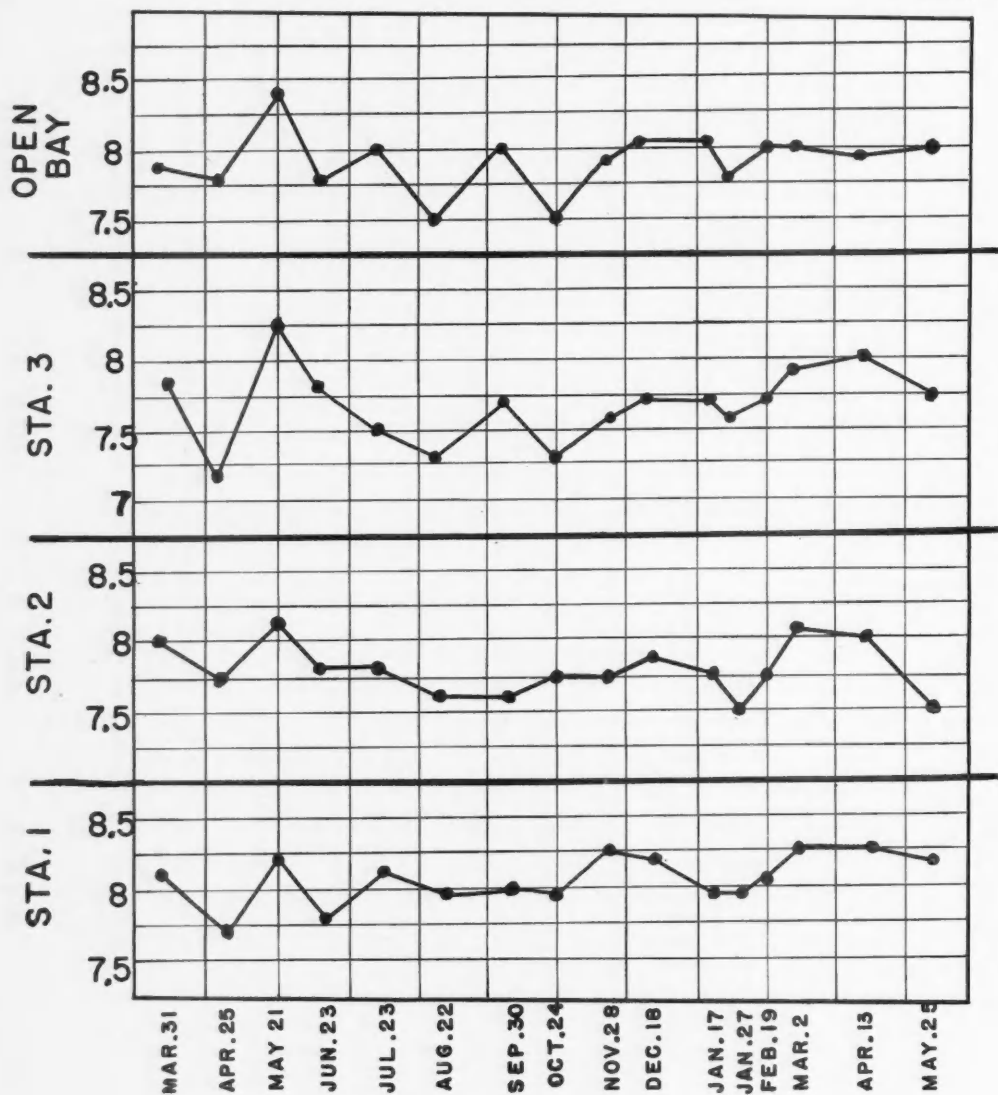FIG. 5. Readings of parts of oxygen per mille at the stations studied.

FIG. 6. Range in pH at the different stations.

SALINITY

The natural beds of oysters in continental United States are found normally in inshore waters of bays and coastal estuaries where there is considerable dilution by inflowing fresh water resulting in changes in salinity. Churchill (1920) in reference to *Ostrea virginica* stated that the oysters can withstand changes in salinity from 2.5 to 33.0 parts per mille, with an optimum of changes from 14.3 to 28.8 parts per mille. In Galveston Bay, Texas, Hopkins (1931) indicated an average salinity of 20 to 30⁰/oo with midsummer lows down to 2 parts per mille. In Long Island Sound, Loosanoff & Engle (1940) reported the summer salinity range of 25 to 32⁰/oo. In Puget Sound, working

with *O. lurida*, Hopkins (1937) found a salinity on the oyster beds of 26 to 29⁰/oo. In an experimental study with *O. gigas* Hopkins (1936) reported optimum feeding activities between 25 and 39⁰/oo.

The ocean waters around Puerto Rico are of a higher salinity than those in many regions where *Ostrea virginica* is found. At Tortugero, on the north coast approximately midway between Arecibo and San Juan, on Oct. 31, 1947, the salinity of the open Atlantic was 37.6⁰/oo; in Boqueron Bay on Oct. 24 (Fig. 7) it was the same, 37.6⁰/oo. On Sept. 16, 1947, at Parguera the salinity was 38.9⁰/oo; at Boqueron on Sept. 30, 1947, it was 36.6⁰/oo. At Ponce on January 24, 1948, the salinity was 33.5⁰/oo
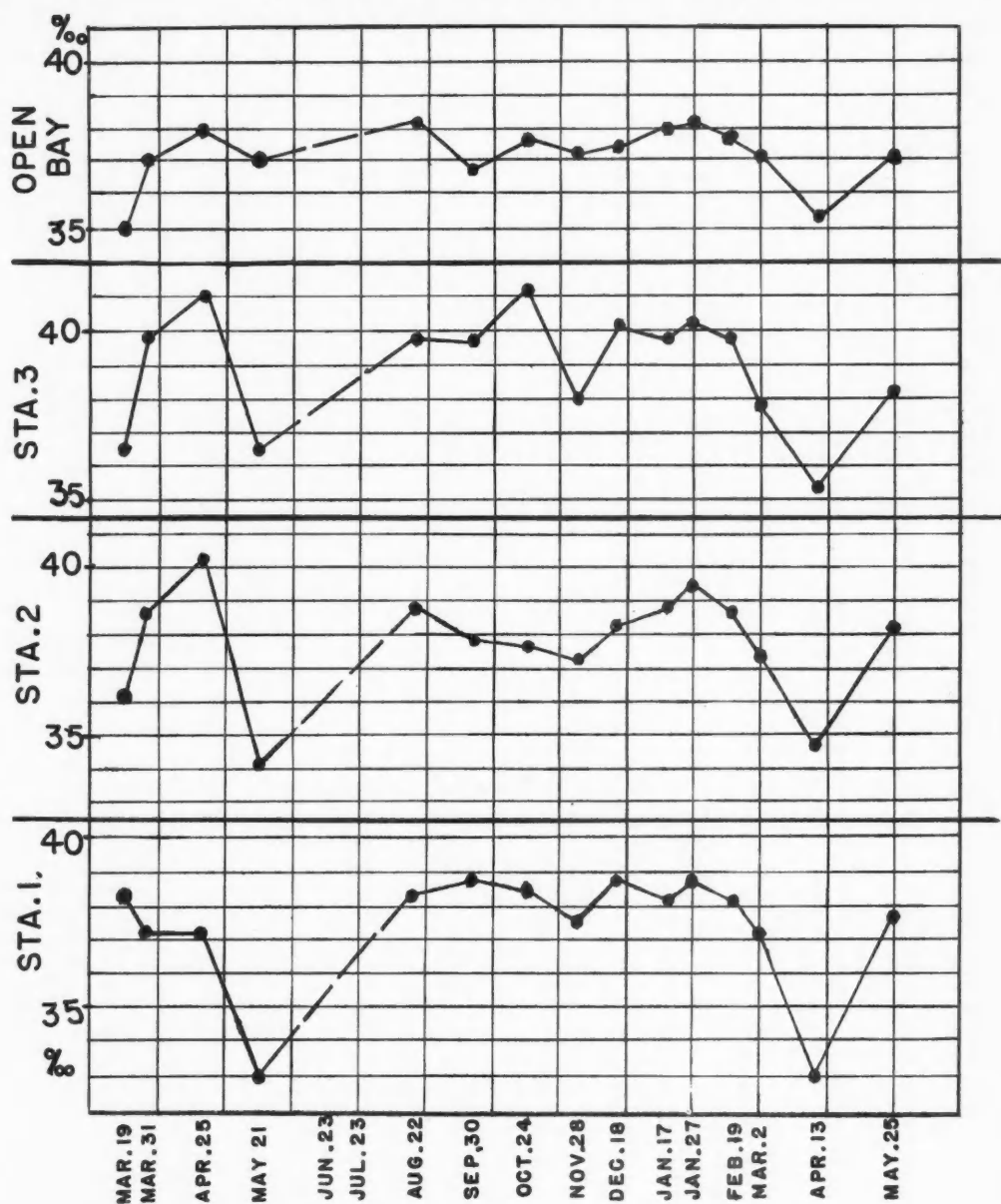
FIG. 7. Fluctuations in the salinity of the waters at the Stations under observation.

while in Boqueron Bay on January 27, 1948, it was 38.2⁰/oo.

The salinity changes in the Bay of Boqueron (Fig. 7) are much the same as those within the lagoon. In the Bay the over-all average of 15 readings was 37.2⁰/oo with the lowest, following spring rains, at 35⁰/oo March 19, 1947. The highest salinity of the surface waters of the Bay of Boqueron was taken after the hot, dry summer season, it was 38.3⁰/oo

on August 22, 1947. The salinity change curve (Fig. 7) follows the general rainfall conditions, as is expected.

Within the lagoon the average salinity changes are greater than in the open bay. This is no doubt due to greater evaporation within the lagoon during dry seasons resulting in higher salinities and more dilution from rains resulting in lower salinities. The average for all stations, 15 readings each, as shown

in Figure 3, was 37.6⁰/oo. At Station 1, the nearest to the open bay, the average of all readings was 37.4⁰/oo with a low of 32.9⁰/oo and a high of 38.9⁰/oo. At Station 2 the average was 37.8⁰/oo, with a low of 34.0⁰/oo and a high of 40.5⁰/oo. At Station 3 average salinity was the highest at 38.0⁰/oo, the low at this station was 34.4⁰/oo and the high 40.2⁰/oo. The salinity differences at the different stations do not seem to be significantly different from each other to account for the differences in concentration of the oysters at the different stations. However, it is possible that the rather uniformly higher, even though slight, salinity at Station 3 may be a factor along with the lower oxygen content and slightly lower pH in limiting the number of oysters at this point.

The highest salinity observed here, in which oysters were living, was taken on May 25, 1948 in a small canal-like ditch where there is no circulation except after heavy rains, a salinity of 44.02⁰/oo was recorded. There were large sexually-matured oysters growing sparsely in this ditch, but apparently normal setting of spats was not taking place as there were no small oysters or spats observed. This high salinity then seems to be an inhibiting factor the same as too low salinity, as shown in many cases (Hopkins 1931) for *O. virginica*.

During normal seasons, when there is sufficient rainfall, fresh water enters the lagoon from a nearby fresh water lagoon, Laguna Cartagena, which is approximately 4 miles to the east of Laguna Rincón. In recent years water from Laguna Cartagena has been used for irrigation thus reducing the flow of fresh water into Laguna Rincón where the oysters are found. The high salinity of this lagoon which may effect the oysters is probably thus developed with a possible increase in salinity if Laguna Cartagena continues to be drained.

BIOLOGICAL OBSERVATIONS

GENERAL BIO-ECOLOGY OF THE LAGOON

A very general bio-ecological survey was made within the areas of the lagoon in which oysters are found. As indicated previously, the dominant plant is the mangrove upon whose aerial roots and low branches the oysters are attached. The observations that have been made were limited to the mangrove association, or area, with the purpose of noting the forms which are competitors with the oysters. Since the oysters rely on the mangrove roots for attachment any plant or animal in competition for this attachment area is important so far as the oysters are concerned. Specimens of the more conspicuous and abundant types were collected for identification and are here listed.

Figure 8 is of a typical mangrove aerial root upon which oysters are growing. As is seen here the lower end of the root, and among the oysters, there are masses of algae of several kinds that cover attachment space on the roots. Most of these algae are limited to the lower ends of the roots and are hence not as important competitors as some animals that live and attach higher up on the roots.

FIG. 8. Photograph of a typical mangrove root upon which oysters are attached. Note that the oysters are concentrated at the upper end of the root, the area within the intertidal zone.

Considering the animals of this association in a phylogenetic order some very important competitors are the sponges. A branching sponge, *Reniera tubifera;* a simple, homocoelid sponge and an encrusting sponge (*Pleraphysilla* sp.) may be considered as dominants. These sponges not only attach to the roots, but also to the surface of the oyster shells; which reduces attachment space for spats. A species of *Pennaria, Bougainvilla* sp., and an *Alcyonium* sp. are the most conspicuous coelenterates of this association. The writer has also found several oysters which were infested with large numbers of an unidentified podocorynid hydroid. These coelenterates seem to be commensal, living attached to the mantle and oral palps of the oysters. Further study of these is being carried on. One flatworm, the polyclad *Pseudoceros superbus*, has been found living on and under the oyster shells. It feeds on dead oysters and other organic matter. Two bryozoans, *Bugula neritina* and an encrusting hippothoid are important and abundant.

Among the several small annelids that live on and among the oysters the most important are the encrusting *Hydroides* sp. and a large tube-dwelling *Sabella* sp. These worms are abundant and definitely

competitors. Another annelid that should be mentioned here is a *Polydora* sp. which lives in nacre covered mud-tubes within the oyster's shell, usually in the left valve. Of the arthropods the only species that is a space competitor is the barnacle *Balanus eberneus* which attaches to the roots and the shells of the oysters. There are numerous decapods living among the mangrove roots. The more conspicuous forms are: the red and white shrimp, *Stenopsus hispidus*; the mud crab, *Panopeus herstii* forma *crassa*; the mangrove crab, *Aratus pisanii*; *Cronius ruber*; *Pachygrapsus gracilis*; *Sesarma ricordi*; *Macroceloma trispinosum*; *Goniopsis cruentata*; and *Eurythium limosum*.

The most important molluscan competitor is *Murex brevifrons*. This snail is the oyster drill of this area and is very common in the Boqueron lagoon. Because of its relatively large size it can be and is picked by the local fishermen, hence is controlled to some degree. Two space competitors are the clams *Melina alata* and *Mytilus hematus*. Oyster spats frequently settle on the large flat shells of Melina, hence gain in the association. *Littorina angulifera* is also found commonly on the roots of the mangrove. It is of general interest to indicate here that at the mouth of the canal, where there are no *O. rhizophorae*, there are found isolated individuals of *Ostrea frons* growing attached to living colonies of the soft coral, *Gorgonia acerosa*. *O. frons* has not been found inside of the lagoon.

The echinoderms found in this association are: *Ophiothrix angulata*, *Ophionereis reticulata*, and *Echinometra viridis*. A group of very important space competitors are the tunicates. The most conspicuous of these are: *Ecteinascidia turbinata*, *Ascidia nigra*, *Perophora* sp., *Botryllus* sp. and *Styela* sp. These species are very abundant in many places and seriously crowd the oysters and cover attachment areas for the setting of spats.

As is seen this mangrove oyster association is a very crowded one. Considering the number and abundance of other species it is obvious that setting spats have considerable competition. The result is that many spats settle on already growing oysters and thus pro-

FIG. 9. Photograph illustrating the crowding of *O. rhizophorae* on the mangrove roots.

duce a crowding and formation of "coon" oyster growth in many areas, as is shown in Figure 9. This crowding also increases the difficulty of harvest, in the selection and picking of the large forms without disturbing young and small oysters.

PLANKTON

From general observations, taken at all seasons, it was observed that plankton organisms were always present in relatively equal quantities. Detailed study of samples showed that the bulk of the samples was composed of diatoms, with members of the genus Thalassiothrix and undetermined filamentous types the most conspicuous. Given in Table 1 are the counts from two representative collections taken at two different seasons, June 23, 1947 and January 27, 1948.

It has been noted that qualitatively these samples do not differ greatly from those reported for the Gulf coast, Long Island, and Chesapeake Bay waters where *O. virginica* beds are found. However, it is of importance to indicate that quantitatively these samples compare very poorly with these areas. The relatively consistent higher temperatures may be the explanation for this phenomenon since the totals more nearly approach the summer counts given for other areas (Galtsoff, et al., 1947) than the very high winter counts found in temperate waters. It is seen

TABLE 1. Counts of plankton organisms taken at Stations 1, 2 and 3 on June 23, 1947 and January 27, 1948. Number per liter given.

Organism	STATION 1		STATION 2		STATION 3	
	6-23-47	1-27-48	6-23-47	1-27-48	6-23-47	1-27-48
Amphiprora	..	2	..	..	..	..
Asterionella	..	..	..	12	..	..
Biddulphia	33	108	..	..	..	..
Chaetoceras	..	700	..	240	..	320
Coscinodiscus	..	12	..	..	..	..
Filamentous algae	765	104	675	112	24	472
Liemophora	..	..	..	4	..	2
Merismopedia	..	..	3	..	..	12
Navicula	33	4	21	32	2	12
Nitzschia	48	6	54	92	72	272
Pediastrum	81	..	..	..	..	..
Pleurosigma	3	..	15	10	6	52
Rhizosolenia	..	72	..	52	..	156
Spirulina	3	..	..	..	..	2
Thalassiothrix	24	670	30	428	2	1,332
Skeletonema	..	248	..	..	26	..
Unidentified cells	..	8	..	6	..	2
Ceratium	..	..	3	..	..	2
Vorticellids	..	22	..	6	..	..
Carchesium	..	..	..	8	..	8
Foraminifera	..	..	3	..	2	..
Tintinnid	..	..	..	2	..	..
Eggs	9	28	9	38	..	6
Hydroid hydranths	45	..	..	6	..	..
Annelid larvae	..	..	6	..	..	..
Bivalve larvae	3	..	3	2	..	..
Copepod	45	6	3	2	4	14
Nauplei	6	2	9	2	4	8
Tunicate larvae	..	..	3	2	..	2
Unidentified Types	15	4	..	2	2	..
Total/Liter	1,110	2,002	885	1,268	142	2,784

here that the January 27, 1948 counts, with a temperature of 26°C., are higher than the June 23, 1947 counts when the temperature averaged 29°C. It should also be noted that very large quantities of detritus of undetermined organic matter is always present in the plankton samples.

Upon examination of the stomach content of several mature oysters it was noted that they contained several species of diatoms, filamentous algae, dinoflagellates, quantities of organic detritus, and in one specimen a zooea crab larva was found. This seems to indicate a lack of selectivity in the feeding of these oysters.

GROWTH STUDIES

In order to obtain records of the relative rate of growth of the oysters in this lagoon two methods were employed. First, relatively isolated individuals growing naturally on mangrove roots were marked and periodically measured. The second method was the measuring of individuals growing on "cultch" shells in a wire mesh basket or on boards suspended among the mangrove roots.

In measuring those individuals naturally attached to mangrove roots measurement was difficult because of the curving of the growing shells following the circular form of the roots. Figure 10 shows curves for the growth of representation individuals which were growing with the anterio-posterior axis following the long axis of the root. Those individuals shown on this diagram, except "ind. x" which was attached to a board, all show more or less the same rate of growth if an average rate is considered. The larger individuals measured between Jan. 17, 1947 to Apr. 25, 1947 show an average daily growth rate of 0.12mm. per day. Those that were first measured when only 7mm. in length (average) on June 23, 1947 until they were 33mm. in length (average) on Jan. 17, 1948 (208 days) show an average, daily growth rate of 0.13mm. per day. It is seen that the early growth period of these individuals was more rapid, possibly because of the slightly higher temperatures.

The individual, "ind. x," growing on the horizontal, flat surface of a board was measured for 156 days of growth, between Mar. 19, 1947 and Aug. 22, 1947, shows an average rate of growth of 0.23mm. per day. This rate of growth is probably greater because it represents summer growth. Also, because the shell was growing upon a flat surface the rate of growth may have been more regularly greater, and measurement more exact.

By extending these growth lines, in Figure 10, back to the date line the approximate age can be determined. It is then readily seen that the rate of growth of these oysters brings them to local market size (approx. 50mm. plus in shell length) within 6 to 7 months. This remarkably rapid growth, which is much greater than in temperate waters, is without doubt a factor which maintains the colony and permits such heavy harvesting the year around.
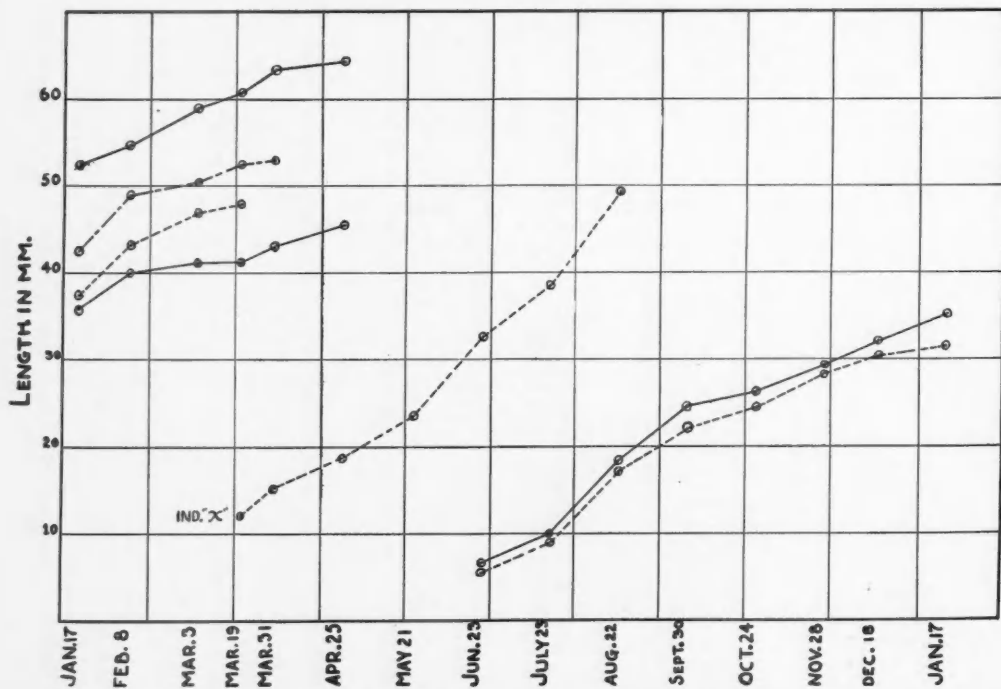
GROWTH OF MARKED INDIVIDUALS

Fig. 10. Growth curves of marked individuals.

The growth and "striking," or setting, of spat was observed at all seasons. Observations were made both from artificially provided "cultch" and the natural setting on the mangrove roots and the shells of larger oysters.

Table 2 is a record of the observations made from collections of individuals brought to the laboratory for study. All measurements are of the length of the dorsal, or right shell of living animals. The number of individuals in each size group is not given here as the number would be variable depending upon the method of collecting the specimens. The collections, in all cases, were made with the primary purpose of securing representative individuals from the different size groups of mature specimens. The smaller size groups were therefore more or less incidental even though the smaller individuals were always found either attached to larger shells or to pieces of mangrove roots brought into the laboratory. Practically all of these individuals were collected at Station 2.

It is readily seen from Table 2 that setting of spats occurs throughout the entire year. From cursory observations there does not seem to be any season during which setting is heavier than in others. Such a study requires further investigation.

TABLE 2. Presence of size groups of oysters taken during different months of the year; # indicates present; –, absence of size groups.

Size range in mm.	January 27 1948	February 19 1948	March 2 1948	April 13 1948	May 25 1948	June 23 1947	July 23 1947	August 22 1947	September 30 1947	October 24 1947	November 28 1947	December 18 1947
1- 5	#	#	#	#	#	#	#	#	#	#	#	#
5-10	#	#	#	#	#	#	#	#	#	#	#	#
10-15	#	#	#	#	#	#	#	#	#	#	#	#
15-20	#	#	#	#	#	#	#	#	–	#	#	#
20-25	#	#	#	#	#	#	#	#	#	#	#	#
25-30	#	#	#	#	#	#	#	#	#	#	–	#
30-35	#	#	#	–	#	–	#	#	#	–	#	#
35-40	#	#	#	–	#	#	#	#	#	#	#	#
40-45	#	#	#	#	–	#	#	#	–	#	#	#
45-50	#	#	#	#	#	#	#	#	#	#	#	#
50-55	#	#	#	#	#	#	#	#	#	#	#	#
55-60	#	#	#	#	–	#	#	#	#	#	#	#
60-65	#	#	#	#	#	#	–	–	–	#	#	#
65-70	#	–	#	#	#	#	#	–	–	#	#	–
70-75	#	#	#	–	#	–	–	–	–	–	#	–
75-80	–	–	–	–	#	#	–	–	–	–	–	–
80-+	–	–	–	–	#	–	–	–	··	#	–	–

The growth of the spats of known age groups was followed by observing individuals setting on cultch of clean Ostrea and Melina shells placed in wire baskets. Figure 11 represents the growth of spats setting and developing on such cultch between Sept. 30, 1947 to January 27, 1948, after which this basket was lost. This represents a period of 120 days during which oysters do not spawn in temperate waters. Six different collections of cultch shells were taken from this basket in order to record the setting and growth of the spats. The spats present were easily divided into size groups which have been taken as age groups or settings of striking spats from different spawn.
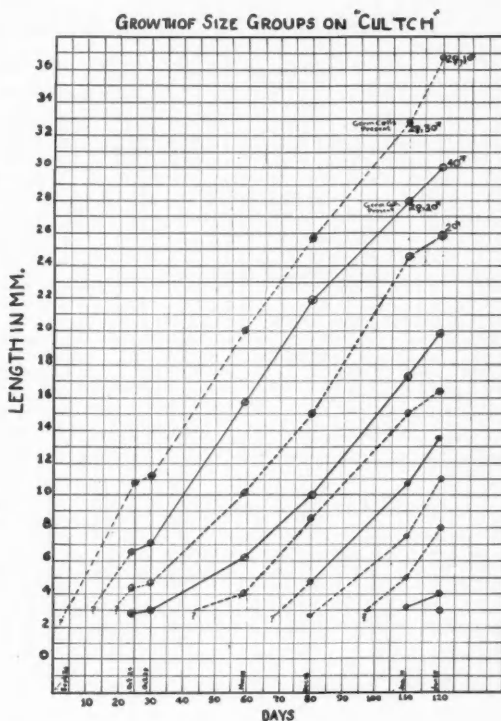

FIG. 11. Growth of spats on "cultch" shells. Presence of mature germ cells is indicated for those 100 days, or more, in age.

On October 24, 24 days after the shells had been placed in the water, there were spats of 4 definite size groups. The largest spats average 11mm. in shell length. The next group averaged 6.9mm., the next 4.5mm. and the smallest size group averaged 2.8mm. On the basis of comparative rate of growth the largest individuals must have set within a day or two after the basket was placed in the water.

Five days later, on Oct. 29, the same 4 size groups were evident with no new groups. On November 28, 59 days in the water, there were 5 size groups present (Fig. 12). After 80 days, Dec. 18, there had been 2 more settings as there were 7 definite size groups.

After 110 days, Jan. 17, 1948, in the water the shells held 9 size groups of young oysters. The largest group, which must have been near 110 days old, averaged 32.7mm. in length. Within this group there were two individuals that held mature egg cells and 3 individuals with active sperm. In the next size group, average 28.0mm. in shell length, and probably only about 100 days old there were 2 individuals with eggs and 2 with active sperm.

To the best of the writer's knowledge this represents the youngest age reported at which oysters become sexually mature.

On January 27, 120 days, there were 10 size groups present of which the larger three groups contained individuals producing sperm as determined by the

FIG. 12. Spat, 59 days old, growing on Melina shells.

smear technic. These individuals were also probably only about 100 days old.

By taking an average of the larger six groups, after the cultch had been in the water 120 days, the average rate of growth was 0.25mm. per day. During these 120 days the environmental conditions varied very little at Station 2, where this basket was located. The temperature averaged 28.0°C., the pH average 7.66, the salinity 38.5°/oo and the dissolved oxygen 5.6°/oo. This was an unusually warm December and January, but the over-all average for the year is near this same figure.

The smallest set spat measured in these observations was 2.0mm. in shell length. From plankton samples straight-line larvae, 0.120mm. in shell lengths, have been taken. The length of larval life and rate of growth of the free-swimming larva have not been determined.

These growth averages are not intended to be mathematically correct, but are given here as representative figures. They were computed simply by dividing the amount of growth by the number of days, the results were then taken as average growth per day. The average rate of growth of these young oysters is greater than that of the large individuals, as pointed out previously. Since the growth studies reported here were carried out during different seasons, which vary very little, it is believed that they are representative.

Sex Studies

As seen from the growth studies spat setting and therefore spawning occurs throughout the entire year in the Boqueron lagoon. For information on gonad development and for records on the sexes animals were examined during all seasons. On each visit to the lagoon small lots of unselected oysters were collected and brought to the laboratory for sex determination. Both the smear method of material from the gonad and histological examination of the gonad were employed. Sixteen collections were made as indicated on

Figure 13. The total number of mature individuals examined was 238 out of which 131 were females and 107 were males, or 55.04% females and 44.95% males.

This ratio of approximately 5 females to 4 males is near the ratio as given for *O. virginica* of nearly equal numbers of the two sexes as found on the Atlantic coast in the Chesapeake Bay and Long Island Sound areas (Loosanoff & Engle 1940). In the Galveston Bay area Hopkins (1931) indicated a ratio of 70.0% females, 20.2% males and 9.1% of doubtful sex, as collected during the spawning season of *O. virginica*.

When the size of the shell of the two sexes is considered it is seen (Figure 13) that the female shells were usually larger, averaging 53mm. in length. The males averaged 45mm. in length of the dorsal or right valve. With few exceptions, in all of the unselected collections, the females tended to be larger as well as slightly more numerous. Those collections in which the males were more numerous and slightly larger are not interpreted as significant when averages are considered. In the collections brought to the laboratory the largest individual studied was a female with a right valve length of 86.4mm. and an over-all shell length of 96.0mm. (Figure 14). The largest male examined had a right valve shell length of 72.0mm. The smallest individuals producing germ cells, as indicated previously, were 27.0mm. with ova and 25.5mm. with spermatozoa.

In the examination of gonad smears and histological studies no individual above 30mm. in shell length was found to be void of sex cells. Active spermatozoa or mature, pear-shaped, ova were always found. Detailed histological studies to determine whether there are recuperation periods or not have not been completed. However, from studies of smears there is no indication of such periods, the production of germ cells seems to be continuous and during all seasons.

On the basis of estimates using the formula given by Galtsoff (1930), and substantiated by the same author (1947), these oysters are capable of producing large numbers of eggs as in *O. virginica*. Galtsoff estimated that an oyster with an ovary 7mm. in thickness was capable of producing 335,000,000 eggs after having spawned 115,000,000 eggs. One female taken from Boqueron lagoon on May 25, 1948 measuring 61.5mm. in shell length had an ovary 3.6mm. in thickness. This individual should then be capable of producing nearly 170,000,000 eggs, on the basis of Galtsoff's formula. Another female with a shell length of 63.0mm., taken November 15, 1946, was producing eggs and had an ovary 2.0mm. in thickness. This individual, taken during the winter season, should then be capable of producing 99,000,000 eggs. The eggs of these oysters have the same diameter as that given for *O. virginica*, 40 microns through the rounded portion of the egg (Galtsoff 1947). The size of the ovary of these oysters referred to here from different seasons is further indication that the production of germ cells is a continuous process, and during a 2 or 3 year life period these animals are potentially able to produce enormous numbers of eggs.
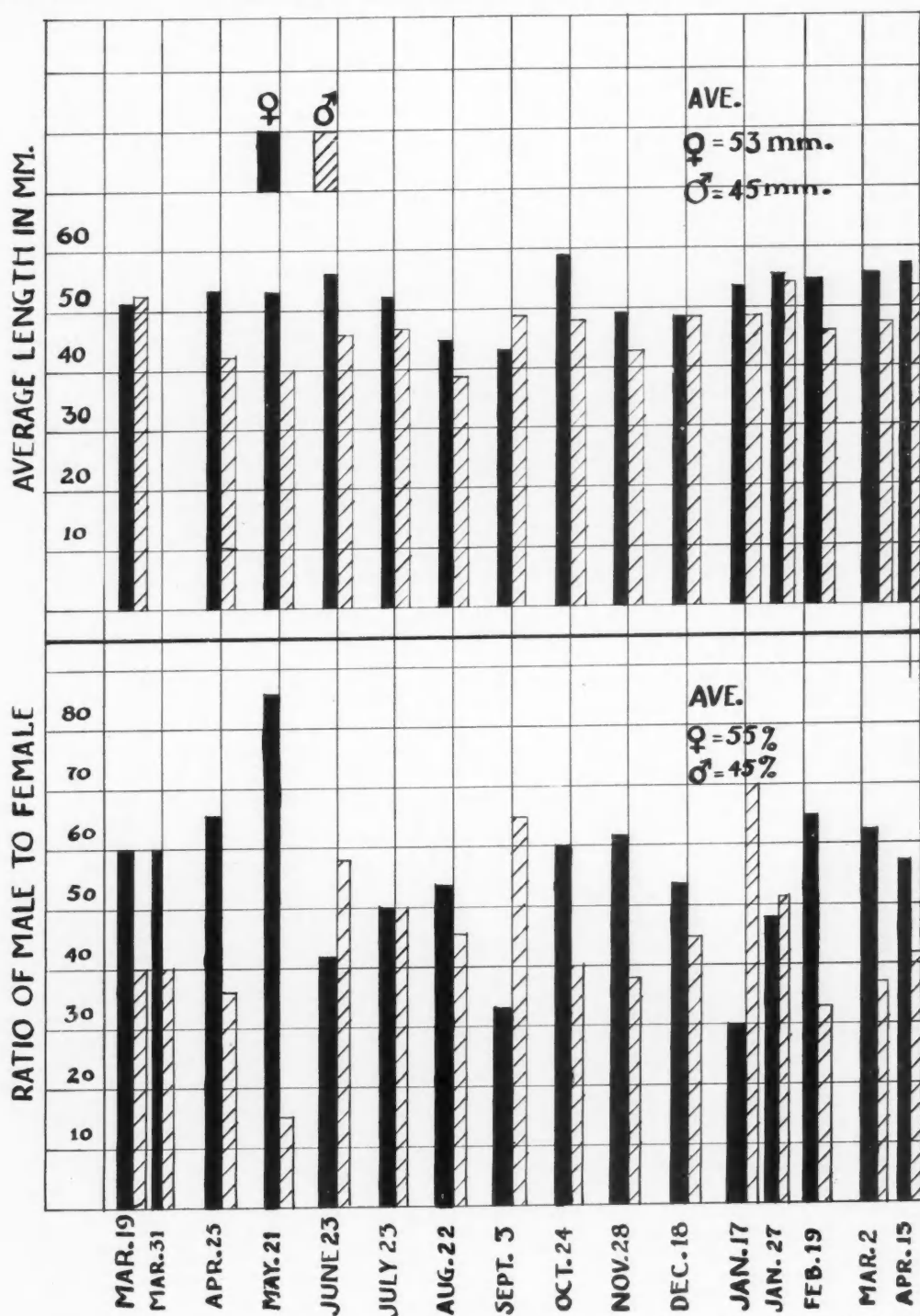
FIG. 13. Upper graph showing average lengths of male to female shells; lower graph showing ratio of male to female animals over period from March 19, 1947 through April 13, 1948.
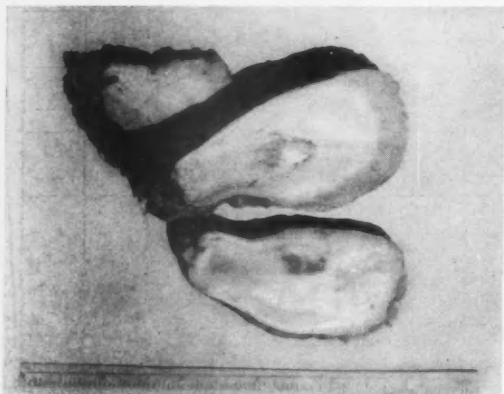
FIG. 14. Adult oyster shell, total shell length 96.0mm.

As pointed out by Galtsoff (1947) the primary significance of such figures, as given above, is not the potential fecundity of the oysters, but rather importance should be placed on the survival of the larvae. Studies to determine this factor have not been completed. However, from the large number of predaceous animals living in association with the oysters, as indicated before, the percentage of larvae that survive is probably small.

There is no indication of protandry in these oysters as in *O. virginica* (Coe 1932) and in *O. lurida* (Coe 1931). Neither is there any indication of sex influence of one sex upon the other. Male individuals have been found attached to the valves of females, females have been attached to males, clusters of all male individuals and clusters of all female individuals have been found. These seem to be normal dioecious animals.

DISCUSSION

In the foregoing account various phases of the ecology of the edible oyster of Puerto Rico, *Ostrea rhizophorae*, have been discussed. In general the hydrographic conditions under which these oysters live are very different from those of *O. virginica*. The salinity of the water is regularly higher and temperatures are consistently higher. The biological environment in which these oysters live is very hazardous with many predators and competitors living among the mangrove roots where the oysters are attached and develop. However, because of a high potential fecundity and a very rapid rate of growth these oysters are able to maintain relatively large numbers, numbers large enough to make them commercially important. From Boqueron Lagoon at least 25,000 pounds (animals with shells) are taken during the period of one year. This biological study, accounted here, may be applied in efforts to maintain or expand this local source of a very good food.

In the local waters oysters do not develop to desirable market size on open shores or in open bays. All of the colonies of importance occur in lagoons where there is no complete turn over or change of the waters during the changes in tides. In these lagoons the oysters are invariably found within the intertidal zone attached to solid objects, chiefly to the aerial roots of the mangrove. The chief reasons for the occurrence of the oysters in these lagoons are probably the concentration of organic food matter, plankton, in the lagoons and also the occasional freshening of the lagoon waters by rains and drainage from fresh water sources. It has been shown that growth and reproductive activities are better in the areas of lower salinity and higher oxygen content. Circulation of fresh water and agitation by winds and currents account for these physical factors.

In view of results from this investigation certain comments and suggestions may be made as to the expansion of the commercial activities of the relatively small oyster industry. First, as pointed out before, the fecundity and rapid growth rate of these oysters permits an all-season industry. However, if the collection of the oysters was systematized so that collections from different parts of the lagoons were made only at regular intervals the size of the oysters would be larger. That is, if the oysters were allowed to grow for longer periods the size would obviously be greater. Market size of 50mm. or more is reached from 6 to 8 months.

It has been shown that spats will attach and develop on any solid object, such as dead shells in baskets or pieces of wood suspended within the intertidal zone. Hence farming cultivation activities are possible if such solid objects were made available as an increase of available attachment surfaces. Set spats could thus be transferred to areas in open waters which are now devoid of attachment areas. The collection of spats on brush or limbs of trees with subsequent transfer to open waters by inserting the brush into the mud bottom would be possible. The building of bottom beds of rocks or dead shells would probably not be possible because of the heavy silting that occurs in these lagoons.

Growth, or farming, areas could also be enlarged or artificially produced by expanding the present limits of existing lagoons if certain biological factors were maintained. Open circulation with bays or estuaries would be essential to maintain plankton populations as well as the important physical factors. Also it would be very important to insure a source of fresh water either from fresh water lagoons or drainage ditches. This is very important in order to restrict the salinity, to keep the salinity down, since evaporation from shallow areas is great in this region. Attachment areas, artificial or natural, would obviously need be supplied. In regard to fresh water sources it should be pointed out that such sources should be maintained in lagoons where oyster colonies now exist. In the case of the Boqueron Lagoon there is danger of depletion of at least part of the existing colony if the water from Laguna Cartagena, a fresh water lagoon, continues to be diverted from the Boqueron Lagoon. It has been observed that the oysters do not set in waters of consistently high salinity of 40⁰/oo or higher.

The other various aspects of the commercial application of this investigation requires further study. The possibilities of developing new oyster colonies in now barren lagoons are very promising.

SUMMARY

1. This investigation was conducted in order to obtain a knowledge of the environmental and biological factors involved in relation to the edible oyster, *Ostrea rhizophorae* Guilding, in the waters of Puerto Rico.

2. The validity of the name *O. rhizophorae* is discussed and the differences between this species and the closely related *O. virginica* are given.

3. These oysters are found mainly in lagoons attached to the aerial roots of the mangrove, *Rhizophora mangle* L.

4. The most important lagoon is the Boqueron Lagoon, which is important commercially.

5. Hydrographic conditions have been studied.

6. Temperatures in the upper 12 inches varied from a low of 25.0°C. to 31.0°C.

7. Dissolved oxygen content varied inversely with the temperatures with a low average of 3.9⁰/oo to a high of 7.0⁰/oo.

8. The pH readings varied from 7.4 to 8.2.

9. The salinity of the lagoon waters is higher than in many areas where oysters grow. It averaged 37.6⁰/oo with extremes of from 32.9 parts per mille to 44.02⁰/oo.

10. In a bio-ecological survey of the oyster-mangrove association the competitors with the oysters are given.

11. Plankton studies have indicated a very low quantitative count. Qualitatively the plankton is rich.

12. Growth records were made of individuals naturally attached to mangrove roots and of spats growing on cultch.

13. The growth rate of large, mature individuals averaged 0.12mm. per day.

14. The rate of growth of spats and young oysters averaged 0.25mm. per day.

15. These oysters reach market size of 50mm. or more within 6 to 7 months.

16. Setting of spats was observed throughout the entire year.

17. Of 238 mature individuals examined for sex, 131 (55.04%) were females and 107 (44.96%) were males.

18. The oysters are sexually active during all seasons.

19. There is no indication of protandry in these oysters.

20. Possible expansion of commercial activities is here discussed.

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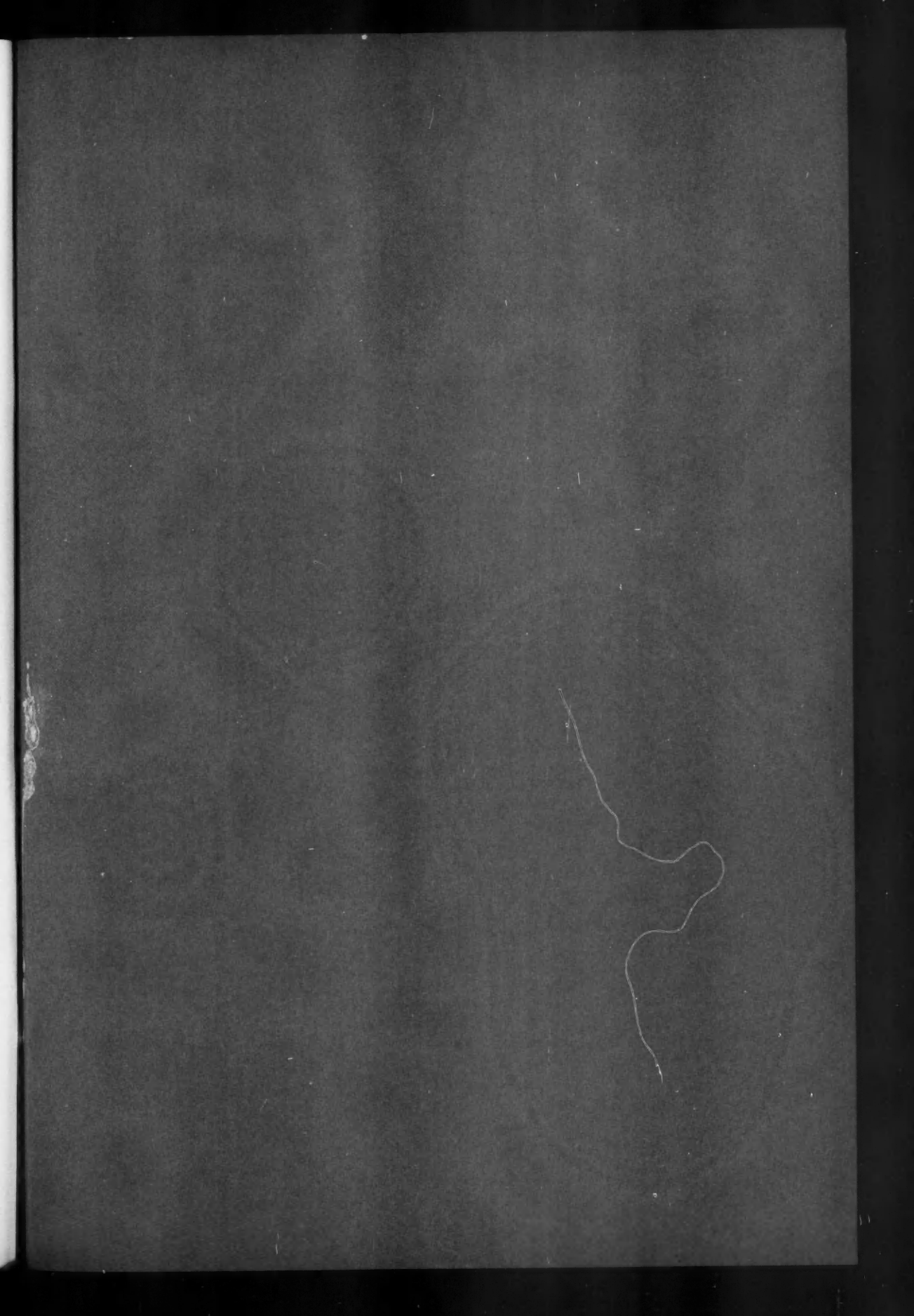
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